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Ford, Amanda; Jouffray, Jean-Baptiste; Norstrom, Albert V.; Moore, Bradley; Nugues, Maggy; Williams, Gareth J.; Bejarano, Sonia; Magron, Frank; Wild, Christian; Ferse, Sebastian

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Amanda K Ford[1,2,3,4]*, Jouffray J-B[3,5], Norström AV[3], Moore BR[6,7], Nugues MM[8,9], Williams GJ[10], Bejarano S[11], Magron F[12], Wild C[2], Ferse SCA[1,2]

[1]Ecology Department, Leibniz Centre for Tropical Marine Research (ZMT), Bremen, Germany; [2]Marine Ecology Department, Faculty of Biology and Chemistry (FB2), University of Bremen, Bremen, Germany; [3]Stockholm Resilience Centre, Stockholm, Sweden; [4]School of Marine Studies, University of the South Pacific, Suva, Fiji; [5]Global Economic Dynamics and the Biosphere Academy Programme, Royal Swedish Academy of Sciences, Stockholm, Sweden; [6]National Institute of Water and Atmospheric Research, Nelson, New Zealand; [7]Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, Australia; [8]EPHE, PSL Research University, UPVD-CNRS, USR3278 CRIOBE, France; [9]Labex Corail, CRIOBE, 98729 Moorea, French Polynesia; [10]School of Ocean Sciences, Bangor University, Anglesey LL59 5AB, UK; [11]Reef Systems Research Group, Leibniz Centre for Tropical Marine Research (ZMT), Bremen, Germany, [12]Pacific Community, Noumea, New Caledonia.

***Correspondence:**
Amanda K Ford
amandakford@hotmail.com

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Abstract

Human activities are changing ecosystems at an unprecedented rate, yet large-scale studies into how local human impacts alter natural systems and interact with other aspects of global change are still lacking. Here we provide empirical evidence that local human impacts fundamentally alter relationships between ecological communities and environmental drivers. Using tropical coral reefs as a study system, we investigated the influence of contrasting levels of local human impact using a spatially extensive dataset spanning 62 outer reefs around inhabited Pacific islands. We tested how local human impacts (low *versus* high determined using a threshold of 25 people km^{-2} reef) affected benthic community (i) structure, and (ii) relationships with environmental predictors using pre-defined models and model selection tools. Data on reef depth, benthic assemblages, and herbivorous fish communities were collected from field surveys. Additional data on thermal stress, storm exposure, and market gravity (a function of human population size and reef accessibility) were extracted from public repositories. Findings revealed that reefs subject to high local human impact were characterised by relatively more turf algae (>10% higher mean absolute coverage) and lower live coral cover (9% less mean absolute coverage) than reefs subject to low local human impact, but had similar macroalgal cover and coral morphological composition. Models based on spatio-physical predictors were significantly more accurate in explaining the variation of benthic assemblages at sites with low (mean adjusted-R^2 = 0.35) rather than high local human impact, where relationships became much weaker (mean adjusted-R^2 = 0.10). Model selection procedures also identified a distinct shift in the relative importance of different herbivorous fish functional groups in explaining benthic communities depending on the local human impact level. These results demonstrate that local human impacts alter natural systems and indicate that projecting climate change impacts may be particularly challenging at reefs close to higher human populations, where dependency and pressure on ecosystem services is highest.

1 Introduction

Humans have become a dominant force of planetary change (Steffen et al., 2007). Ecosystems worldwide are being fundamentally altered by climate change impacts against a diverse backdrop of local anthropogenic stressors. Our ability to reliably predict the future configuration of affected ecosystems requires a thorough understanding of interactions between these different stressor types (Williams et al., 2019). Increasing evidence indicates that ecosystems are being reorganised, or homogenised, into stress-tolerant or opportunistic communities, leading to novel systems that differ from their previous state in terms of their dominant constituents (Graham et al., 2014; Morse et al., 2014). Quantifying ecological reorganisation over broad scales remains challenging due to coarse taxonomic resolution inherent to large datasets that are necessary to address this topic. Nonetheless, this phenomenon may significantly alter a system's relationship with various environmental and climate change-related drivers (Côté and Darling, 2010; Williams et al., 2015a). Understanding what role local human impacts play in driving ecological reorganisation and changing a system's relationship with its biophysical environment is thus pivotal to improving predictive models and informing local management (Robinson et al., 2018; Jouffray et al., 2019; Henderson et al., 2020).

Inherent high biodiversity and the presence of multiple stressors acting at local and global scales make tropical coral reefs a unique system to examine how local human impacts drive ecological states (Hoegh-Guldberg et al., 2007; Ban et al., 2014; Norström et al., 2016; Darling et al., 2019). Locally, rapidly expanding coastal development, sewage input, and agricultural practices are reducing water quality, whilst the modernisation of fishing gear and expedited market access are facilitating overexploitation of coastal fisheries resources (Fabricius et al., 2005; Brewer et al., 2012; Hamilton et al., 2012). Globally, the intensity and frequency of thermal anomalies, unusual weather patterns, and destructive storm events are increasing (Gattuso et al., 2015; van Hooidonk et al., 2016; IPCC, 2019), and recovery windows between stress events are narrowing (Riegl et al., 2013; Hughes et al., 2018). The productivity and provision of ecosystem services (e.g. Woodhead et al., 2019) of coral reef benthic communities differ depending on their composition (Ferrario et al., 2014; Rogers et al., 2018), underlining the importance of quantifying how communities are affected by global change. The widespread negative effects of climate change-related stressors are relatively well-understood. However, despite more than half the world's coral reefs being located within 30 minutes travel time from human populations (Maire et al., 2016), the role of local stressors remains somewhat contested. These local stressors can range greatly in their intensity depending on inherent factors such as human population density and the level of exploitation, such as reliance on marine resources.

Higher human population densities have been linked to reductions in reef fish biomass and coral cover, and to increases in fleshy (turf and macro-) algal cover (Sandin et al., 2008; Williams et al., 2015b; Heenan et al., 2016; Smith et al., 2016). However, coarse taxonomic resolution (inherent to large-scale datasets) can lead to the conclusion that there is no link between local stressors and reef condition (e.g. Bruno and Valdivia, 2016). This may be a particular issue in regions such as the tropical Pacific where species diversity is exceptionally high and fleshy macroalgae,

frequently stated as principal alternative organisms on degraded reefs, do not play such a dominant role in benthic dynamics compared, for instance, to the Caribbean region (Roff and Mumby, 2012). Furthermore, reefs are increasingly existing in a partially degraded condition between distinct regimes (Mumby, 2017), likely having undergone ecological homogenisation resulting from the non-random removal of species with particular traits in response to environmental factors (McWilliam et al., 2020). In this case, coral cover can remain moderate but comprises a less diverse community of stress-tolerant and opportunistic types (Côté and Darling, 2010; van Woesik et al., 2011; Riegl et al., 2013). Ecological homogenisation is visible across reef habitat types, with inshore reefs that are naturally exposed to a more challenging environment (e.g. in terms of light, temperature, and sediment input) favouring a smaller species pool of stress-resistant corals compared to nearby outer reef habitats (Rogers, 1990; Browne et al., 2013; Williams et al., 2013; Schoepf et al., 2015; Morgan et al., 2016).

A recent study demonstrated that whilst sea surface temperature (SST), chlorophyll concentration, and wave energy have strong power in predicting benthic assemblages at remote reefs, this predictive power is lost or the relationships fundamentally altered at reefs closer to human populations (Williams et al., 2015a). Considering the dominant role of humans in shaping ecosystems, factors associated with local anthropogenic impacts may have overtaken biophysical drivers in structuring these altered reefs. It has also been postulated that reorganisation towards a stress-tolerant coral community could increase resilience to climate change, assuming co-tolerance between local and climate change-related stressors (Côté and Darling, 2010), in line with the concept of 'intrinsic resistance' (Darling and Côté, 2018). Indeed, coral richness does not translate into higher resilience to disturbances (Zhang et al., 2014). Better understanding and accounting for the role that local human impacts play in shaping benthic communities and their relationships with environmental drivers is important for developing theories, designing experiments, setting baselines, informing management, as well as optimising large-scale spatial predictive models for coral reef futures.

Here, we investigate how local human impacts affect coral reef benthic communities in the tropical Pacific. We start by classifying 62 island sites into two levels of local human impact (low *versus* high) using a set threshold of human population density informed by previous work (i.e. D'agata et al., 2014). We then ask whether the level of local human impact influences benthic community structure or the relationship between benthic community structure and spatio-physical explanatory drivers. Lastly, we examine the relative roles of ten biophysical parameters as drivers of benthic community structure under low *versus* high local human impacts. We hypothesised that spatio-physical drivers would be more related to benthic community structure on reefs exposed to low local human impacts compared to those with high local human impacts, where we expect human-associated factors to have become more dominant. This approach allowed us to develop on the findings of Williams et al. (2015a) by testing whether decoupling between reefs and biophysical drivers in the presence of humans was also detectable between different levels of local human impact.

2 Material and methods

2.1 Study area and sampling design

This study intended to build on work from Williams et al. (2015a) by assessing in more detail how local population density, rather than human presence/absence, potentially decouples the relationship between reef benthos and larger-scale environmental drivers. To do so, we utilised a large-scale dataset that is unique in having both site-level ecological (fish and benthic) and socio-economic data (in particular human density per reef area at the site level), which is missing from other datasets that rely on global socioeconomic estimates for human population density, or in some cases district-level surveys. Fish and benthic communities at 62 reefs within 17 different Pacific Island countries and territories were surveyed once between 2003–2008 (see Supplementary Figure 1 for map) as part of the Pacific Regional Oceanic and Coastal Fisheries Development Programme (PROCFish/C/CoFish) under the auspices of the Pacific Community. Importantly, all reefs were in close vicinity to, and used by, coastal human communities across a large range of intensities (e.g. relative human density ranged from 1.3–1705 humans km^{-2} reef). For site disturbance history, sampling dates and detailed sampling methodology, refer to Supplementary Table 1 and Pinca et al. (2010). Though it is important to acknowledge that the sampling program was not originally designed in a way to address macroecological questions or aggregate beyond the state/territory level, we did our best to account for the shortcomings in the design by including additional information such as observer bias (see section 2.3 for details on environmental parameters included). Furthermore, while data may not be representative of the current-day scenario, it is the trends that are important for this study. Accordingly, we are confident that despite some inevitable compromising, this gave us the best possible dataset to look at the effects of site-specific human density.

2.2 Field surveys

Underwater surveys covered outer (fore-) reefs, with on average nine (n = 3–47) joint fish-benthic 50 m transects measured at each site. Transect data were pooled within each site. Reef fish communities were measured using the variable distance-sampling underwater visual census method along transects (described in Labrosse et al., 2002). Data on abundance and size were recorded to species-level for herbivorous fish. Counts were converted to biomass (g m^{-2}) from established length-weight relationships (Kulbicki et al., 2005). Benthic cover data was obtained using the medium-scale approach described by Clua et al., (2006). This method is based on a semi-quantitative description of ten 25 m^2 (5 x 5 m) quadrats laid down on each side of the 50 m transect (i.e. 20 replicate quadrats / 500 m^2 per transect). Surveyors first recorded abiotic and live coral substrates, i.e. sand, rubble, rocky slab, boulders, and hard coral - live, bleached, and long dead, with live coral divided into broad morphologies (e.g. branching, encrusting, massive). Each component was quickly estimated using a semi-quantitative scale ranging from 0 to 100% per quadrat, in units of 5%. Secondly, benthic groups (e.g. macroalgae – inclusive of calcified and fleshy types, turf algae, crustose coralline algae [CCA], sponges, cyanobacteria) growing over abiotic substrate such as long dead coral were recorded using the same semi-quantitative scale (Table 1).

Fishing grounds were initially delineated from information given by local fishers and quantified from satellite interpretations (similar to methods in Close and Hall, 2006; Léopold et al., 2014). Total reef area (km^2) within each fishing ground was then derived from reef areas quantified by the Millennium Coral Reef Mapping Project from satellite images (Andréfouët et al., 2006). Socioeconomic assessments determined total population within communities with access to the fishing ground, allowing subsequent calculation of human population relative to reef area (referred to as 'relative human density'). Finfish landings for each site, determined from interviews with fishers, were extrapolated to total finfish catch per year per reef area ('relative fishing pressure') (see Pinca et al., 2010).

Table 1 Benthic variables included in the models and their ranges.

Variable	Description	Range (%)
live hard coral	mean cover (%) of live hard coral	6.1–65.1
dead hard coral	mean cover (%) of dead hard coral; including rubble, boulders, and pavement. Dead hard coral may also include biotic groups (i.e. growing over the dead coral), which are further classified as additional categories below*	5.5–61.2
branching morphologies	proportion (%) of branching coral morphologies within live hard coral community	0.1–85.6
encrusting morphologies	proportion (%) of encrusting coral morphologies within live hard coral community	2.8–72.9
massive morphologies	proportion (%) of massive coral morphologies within live hard coral community	0.1–60.6
CCA	mean cover (%) of crustose coralline algae	0.2–43.5
macroalgae	mean cover (%) of macroalgae; inclusive of calcified and fleshy types	0.0–31.2
turf algae	mean cover (%) of turf algae	0.0–45.6

**not all categories are mutually exclusive – abiotic (e.g. dead coral, sand) and live coral substrates were recorded up to 100%, and biotic cover (e.g. algal groups) was recorded separately up to 100% (i.e. sum of substrate and biotic cover ≠100%).*

2.3 Data analyses

2.3.1 Response variables

As response variables, we selected the main benthic groups (i.e. those with a mean composition >10% of benthic community): dead coral (incorporating long dead coral,

rubble, boulders, and pavement), live hard coral, and algal groups (differentiating turf algae, macroalgae, and CCA). We also assessed the proportional representation (within the live hard coral community) of the three most commonly observed morphological groups: branching, encrusting and massive morphologies. Pairwise relationship tests (*corvif* function – Zuur et al., 2009) established no collinearity among the response variables (correlation; $R^2 < 0.5$). Table 1 provides an overview of the benthic variables and their ranges.

2.3.2 Model predictors

We had to make a feasible choice of how to determine low *versus* high impact sites. Rather than choosing a completely arbitrary threshold, we selected one that was informed by previous findings by D'agata et al., (2014) – using boosted regression trees for the same dataset, the authors identified 25 people km^{-2} reef to be the threshold after which taxonomic diversity of parrotfishes significantly declined. We then ran a sensitivity analysis to demonstrate how robust our findings were (see section 2.3.4). To compare reefs exposed to different disturbance regimes, we thus categorised all sites into those subject to low (i.e. < 25 people km^{-2} reef; n = 29) and high (i.e. > 25 people km^{-2} reef; n = 33) local human impact. Relative human density correlates with relative exploitation – i.e. relative human density was collinear (R^2 = 0.8) with fishing pressure (tonnes fish km^{-2} reef $year^{-1}$; Table 2). This threshold was also a median point and allowed similar sample sizes in each impact level (see Supplementary Figure 2). Relative human density also showed weak positive correlation with market gravity – an index combining the population size of nearby human settlements and their accessibility to reefs (Cinner and Maire, 2018; Cinner et al., 2018). However, we decided to base our study on relative human density as we had unique site-level data and we see this metric to be more directly linked to benthic communities in terms of human density-dependent sewage and agricultural run-off in addition to subsistence and artisanal fishing.

The selected biophysical predictors included a variety of factors that were either collected during field surveys or extracted from public data repositories (Table 2). Due to inherent differences in coral reefs across latitudinal scales (e.g. Hughes et al., 1999; Harriott and Banks, 2002), latitude was represented by degree distance from the equator without differentiating between north and south (0–23.9°). Degree heating weeks (DHW) data were extracted from the NOAA Coral Reef Thermal Anomaly Database (CoRTAD version 4 - Casey et al., 2012)). Storm exposure was quantified from the NOAA IBTrACS-WMO data (Knapp et al., 2010a, 2010b) within ArcMAP 10.4 (ESRI, 2011), where the number of storms (categories 1–5 on the Saffir-Simpson Hurricane Scale) passing within a 50 km radius of each site (Behrmann projection) was extracted. Storm exposure and DHW data were confined to 12 years prior to each respective site's survey date based on the premise that remote reefs can recover from acute disturbances within this timeframe (Sheppard et al., 2008; Gilmour et al., 2013). Reef depth, estimated during field surveys, was averaged over all transects at each site. Island relief refers to each site's geomorphology, and was classified into three categories: atoll, low-lying island, and high island based on available information (see Supplementary Table 1 for references), and authors' knowledge. Island relief was included as a predictor due to its known influence on coral reef benthic and fish communities (Donaldson, 2002; Houk et al., 2015). Herbivorous fish from selected families (e.g. excluding

herbivorous damselfish) encountered during visual surveys were classified into functional groups according to Heenan et al. (2016) (see Supplementary Table 2). Biomasses (g m^{-2}) of the following functional groups were then incorporated as predictors: browsers, grazers, detritivores, scrapers and small excavators, and large excavators and bioeroders. Market gravity (Cinner and Maire, 2018) was extracted for each site in QGIS (QGIS Development Team, 2019) and was incorporated as a continuous predictor.

Prior to model fitting, paired plots were assessed for collinearity between model terms. Strong collinearity (R^2 > -0.9) between latitude and DHW precluded their joint inclusion in subsequent models, and consequently latitude was selected because of its complete reef-specific dataset (DHW data limited to n = 55 sites). Multi-collinearity was also then tested using the generalised variance inflation factor (*GVIF*) function (*car* package - Fox and Weisberg, 2019) where values >3 suggest collinearity – as a result longitude was excluded from all models and the joint inclusion of browsers and scrapers was prohibited (i.e. individual best-fit models were constrained to contain only one or the other).

2.3.3 Statistical models

All statistical analyses were performed in R version 3.6.1 (R Development Core Team, 2019). Differences in benthic community structure between reefs exposed to low *versus* high local human impact level were tested using *t*-tests with appropriate variance structures depending on homogeneity of variance test outcomes. Due to surveyor discrepancies in recording turf algal cover, we created a random effect (*bias_score*) to be incorporated within turf algae models (see Supplementary Figure 3 for details). No surveyor-related discrepancies were evident for other benthic groups (see Supplementary Figure 3). To test how turf algal cover differed across the two local human impact levels we thus used a linear mixed effects model incorporating *bias_score* as a random effect. All hereon described models were run separately for sites predetermined to be exposed to either low or high local human impacts to explicitly test for decoupling of abiotic and biotic predictors under different disturbance regimes.

To test whether the level of local human impact influences the relationship between benthic community structure and spatio-physical explanatory drivers, we developed a 'spatio-physical' model (i.e. focusing on spatial and physical predictors only) that included storm exposure, reef depth, latitude, and island relief. To account for non-linear relationships between response variables and predictors, we applied generalised additive mixed effects models (GAMM) using the (Wood and Scheipl, 2014) and *lme4* packages. To account for possible spatial autocorrelation, ten unique island clusters (*cluster*) were identified and incorporated into models as a random effect (for details see Supplementary Figure 4). For turf algae models, *bias_score* was additionally included as a random effect. To avoid overfitting, the number of knots within models was limited to four. We retained the adjusted-R^2 (Adj-R^2) values from the model output to quantify each model's explanatory power. Adj-R^2 values for each response variable were then compared (by paired *t*-tests) to test overall differences in model performance in explaining benthic community structure under the two local human impact levels.

363 **Table 2** Predictor descriptions and ranges at outer reefs. [a] predictor incorporated in
364 'spatio-physical' models; [b] predictor used in model selection procedures. For sources
365 of data, see main text.
366

Predictor	Description	Range
reef depth [a,b]	mean depth (m) of transects	3.9–10.5
degree heating weeks (DHW)	measure of cumulative thermal stress – sum of previous 12 weeks where thermal stress anomaly ≥ 1°C; value averaged over 12 years preceding survey; negatively collinear (R^2 = -0.9) with latitude; only available for n = 55 sites	0.6–3.5
latitude [a,b]	degrees (°) distance from equator (absolute value). Negatively collinear (R^2 = -0.9) with DHW	0.0–23.9
longitude	degrees (°) longitude on continuous scale (i.e. -175 counted as 185), included to account for distance from the Coral Triangle biodiversity hotspot	134.3–214.2 (i.e. -145.8)
storm exposure [a,b]	total number of storms (cat. 1 to 5 on the Saffir-Simpson Hurricane Scale) passing within 50 km of site within previous 12 years	0–14
relief [a.b]	3 classifications: 1 = atoll; 2 = low-lying island; 3 = high island	
browser biomass [b]	biomass (g m^{-2}) of browsers	0.1–58.5
detritivore biomass [b]	biomass (g m^{-2}) of detritivores	0.5–62.8
excavator biomass [b]	biomass (g m^{-2}) of large excavators and bioeroders	0.0–369.1
grazer biomass [b]	biomass (g m^{-2}) of grazers	1.1–161.0
scraper biomass [b]	biomass (g m^{-2}) of scrapers and small excavators	1.9–134.3
relative human density	number of people within communities of the primary/customary resource users (living adjacent to/accessing fishing grounds within the reef area) related to total reef area (people km^{-2} reef), positively collinear (R^2 = 0.7) with relative fishing pressure. Used to determine local human impact level	1.3–1705
relative fishing pressure	annual reef finfish catch (tonnes) km^{-2} reef $year^{-1}$; positively collinear (R^2 = 0.8) with relative human density	0.1–78.2

market gravity [b]	index that combines human population size and reef accessibility	0–1140

Lastly, to examine the relative roles of ten biophysical parameters as predictors of benthic community structure under low versus high local human impacts, we applied model selection techniques using the *MuMIn* package (Barton, 2016). From an initial model containing ten biophysical predictors (i.e. those included in the 'spatio-physical model' as well as biomass of herbivorous fish functional groups, and market gravity – see Table 2), the dredge function was used to run all possible predictor combinations and rank models from best to worst based on Akaike weight. The function also returns a value between 0 and 1 for each predictor that reflects its relative importance (RI), representing the total Akaike weight of all models containing that predictor (i.e. higher values correspond to greater RI). Output models were restricted to comprising a maximum of four predictors. One sample (Niue) was removed from the model selection procedure due to a lack of data for market gravity (i.e. n = 61). Model selection was run separately for sites with low and high levels of local human impact, and all models incorporated the *uGamm* wrapper function to allow the inclusion of random effects consistent with 'spatio-physical' model constructions. To assess incongruities between benthic communities exposed to different local human impact levels, we retained the 'best-fit' model structures (i.e. all predictors included in models with Akaike weight >0.05) for each benthic response variable, as well as the RI of individual predictors.

2.3.4 Assumptions and sensitivity tests

All response variables were logit-transformed (appropriate for percentage data - Warton and Hui, 2011) using the *car* package, following adjustment using each respective variable's minimum value >0. All model predictors were standardised (*z*-scores) to allow comparisons between predictors with largely varying effect sizes and numeric values (Zuur et al., 2009). Model residuals were checked for the violation of model assumptions using the *gam.check* function (see Supplementary Figure 5). As part of a sensitivity analysis, 'spatio-physical' models were additionally run using ± 5 and ± 10 humans km^{-2} reef as a threshold from which to categorise 'low' and 'high' impact sites, with consistent outcomes observed (see Supplementary Table 3). Furthermore, we repeated the same for a range of thresholds based on human density relative to outer reef area (as opposed to full reef area), again with consistent outcomes observed (see Supplementary Table 4).

3 Results

3.1 Benthic assemblages under contrasting local human impacts

Benthic communities subject to high local human impact were associated with lower live hard coral cover (-9.2% mean absolute coverage; *t*-test: $p = 0.002$; Figure 1A). However, the relative contribution of different coral morphologies within the live hard coral community did not differ significantly with local human impact level (Figure 1B). The only algal group that differed significantly depending on the local impact level was turf algae, which was higher under high local human impact (+10.7% mean absolute coverage; linear mixed effects model: $p = 0.015$; Figure 1C).

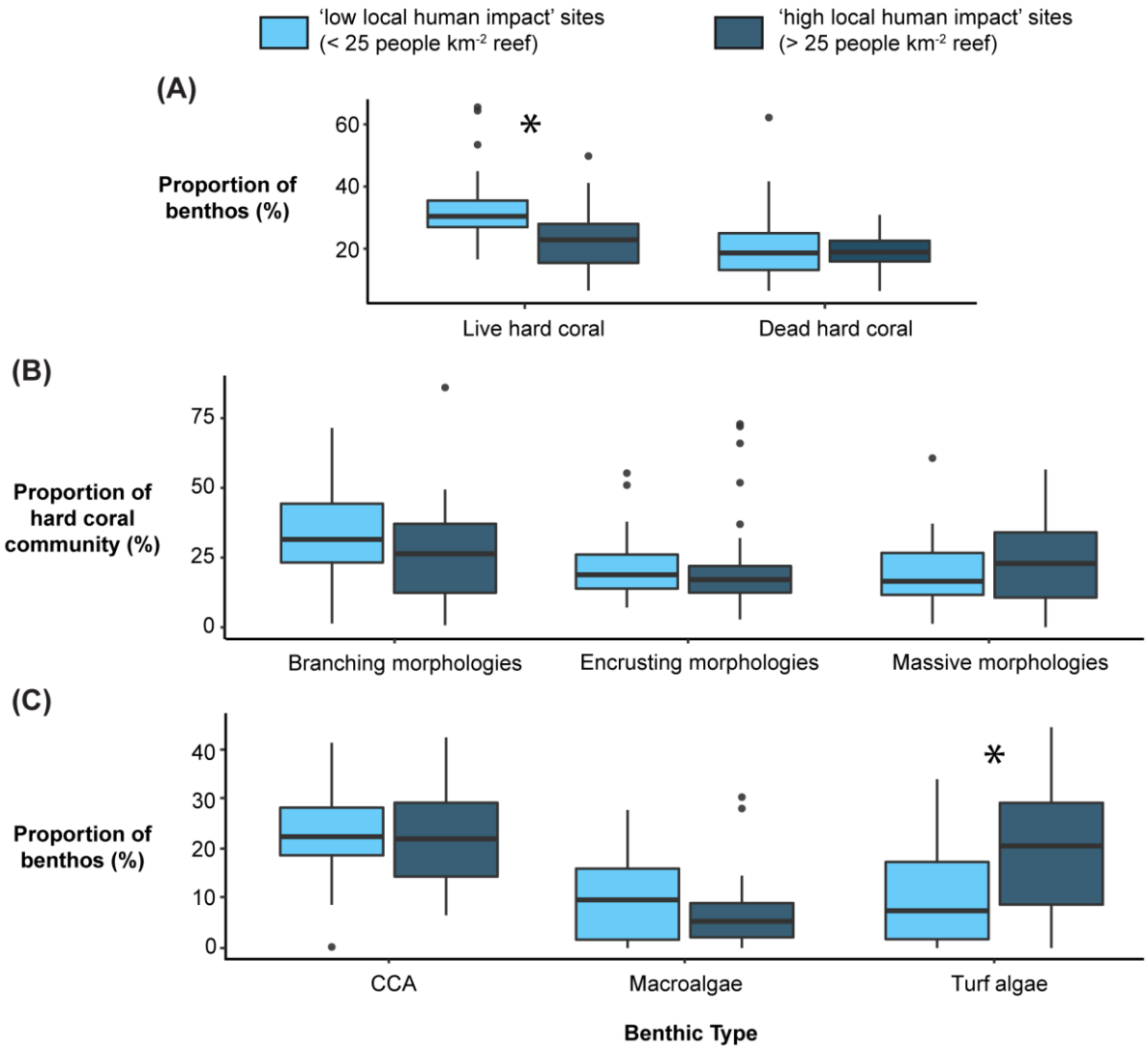


Figure 1 Boxplots detailing (**A**) benthic cover (%) of substrate types (from left to right; live hard coral, dead hard coral), (**B**) the relative proportion (%) of the three most dominant morphologies in the live hard coral community (branching, encrusting, massive), and (**C**) benthic cover (%) of different algal groups (CCA, macroalgae, turf algae), at sites determined to have low or high local impacts. Asterisk (*) indicates significant differences ($p < 0.05$) in cover of the respective benthic variable between local impact levels according to two-sample *t*-tests, or for turf algae according to linear mixed effect models incorporating *bias_score* as a random effect (see section 2.3.2).

3.2 Predictive strength of 'spatio-physical' model

The pre-defined 'spatio-physical' model exhibited relatively high power in explaining benthic assemblage variance at sites with low local human impacts (mean Adj-R^2 ± SE; 0.35 ± 0.09; Figure 2), but model performance was severely compromised when local human impacts were high (0.10 ± 0.04; paired *t*-test: $p = 0.01$). When considering only the substrate types and dominant morphological groups (i.e. without the algal groups) the mean adjusted-R^2 for sites with low local human impacts increases to 0.44 ± 0.06 but stays unchanged at sites with high local human impacts.

When local human impacts were low, 'spatio-physical' predictors explained a high proportion of the variance of live hard coral (Adj-R^2 = 0.52) and macroalgae (Adj-R^2 = 0.59) cover, and the relative contribution of branching (Adj-R^2 = 0.64) and massive (Adj-R^2 = 0.50) coral morphologies. Conversely, these variables were consistently poorly explained when local human impacts were high (Adj-R^2 = 0.00, 0.26, 0.17, 0.10, respectively). No variance in turf algae was explained by this model for reefs at either local human impact level. Significant differences in the power of the 'spatio-physical' model in explaining benthic assemblage variance between 'low' and 'high' impact sites held constant when the threshold was moved ± 5 and 10 humans km^{-2} reef (i.e. paired *t*-test: $p < 0.05$; Supplementary Table 3).

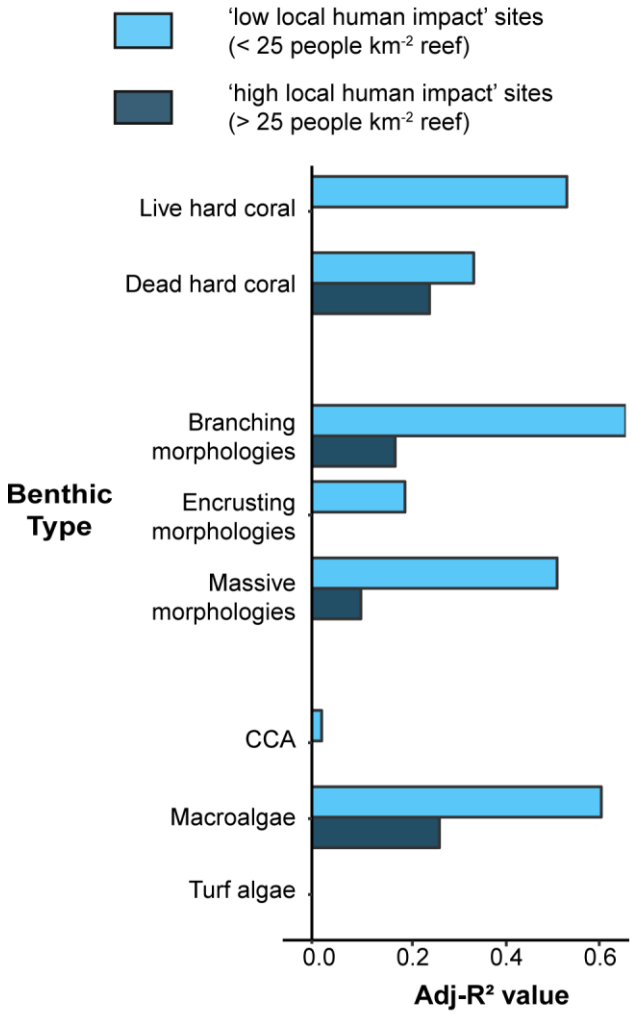
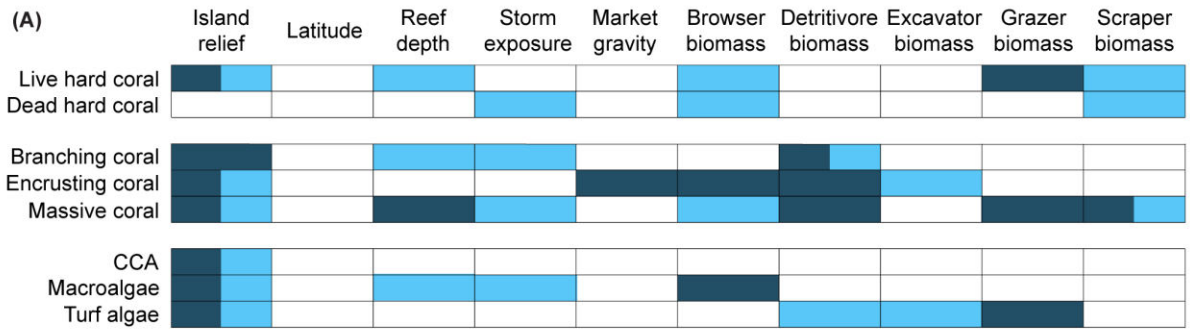


Figure 2 Explanatory power (Adj-R^2) of the 'spatio-physical' model (including the predictors storm exposure, reef depth, latitude, and island relief) in predicting individual benthic responses (live hard coral, dead hard coral, the proportion of branching, encrusting, and massive morphologies, and cover of algal groups CCA, macroalgae, and turf algae). Bars are absent where the Adj-R^2 value = 0.

3.3 Relative importance of predictors

Best-fit' models tailored for each individual benthic variable comprised distinctly different predictors depending on the level of local human impact (Figure 3A). Two of the predictors where discrepancies were most apparent were storm exposure and

grazer biomass, which were only selected for 'best-fit' models at sites with low and high local human impacts, respectively. Similarly, reef depth was selected as part of 'best-fit' models for more response variables (live hard coral, branching morphologies, and macroalgae) at sites with low local human impacts. Further discrepancies under the two levels of local human impact were revealed by comparing the mean RI of each predictor (Figure 3B,C), as the RI trends for predictors almost reversed between low *versus* high local human impact sites. At sites with low local human impacts, the individual predictors with the highest RI in explaining benthic communities were storm exposure, scraper biomass, island relief, followed by reef depth (Figure 3B). Contrastingly, apart from island relief which was on average the most important predictor, storm exposure, scraper biomass, and reef depth were among the least important predictors when local human impact was high (Figure 3C). For benthic communities exposed to high local human impact, biomass of grazers, detritivores, and browsers, as well as market gravity, ranked as the most important predictors of benthic community structure.



(B)

Predictor	RI
Storm exposure	0.288
Scraper biomass	0.250
Island relief	0.244
Reef depth	0.138
Browser biomass	0.086
Detritivore biomass	0.079
Excavator biomass	0.047
Latitude	0.040
Grazer biomass	0.031
Market gravity	0.023

(C)

Predictor	RI
Island relief	0.195
Browser biomass	0.096
Market gravity	0.084
Detritivore biomass	0.075
Grazer biomass	0.074
Latitude	0.044
Reef depth	0.042
Scraper biomass	0.041
Storm exposure	0.038
Excavator biomass	0.030

Figure 3 (**A**) Outcome of model selection procedures: coloured boxes indicate that the predictor was selected for 'best-fit' models (i.e. those with Akaike weight > 0.05) at sites subject to low and/or high levels of local impacts. The overall mean relative importance of each predictor (RI - based on total Akaike weight of all models including that predictor) in explaining the benthic response variables is shown separately for sites subject to (**B**) low and (**C**) high local impacts. Note: though model selection was limited to four predictors per model, all predictors included in models with Akaike weight >0.05 are shown meaning there may be more than four predictors shown within one impact level for a response variable. Model outputs for 'best-fit' models are available in Supplementary Table 5.

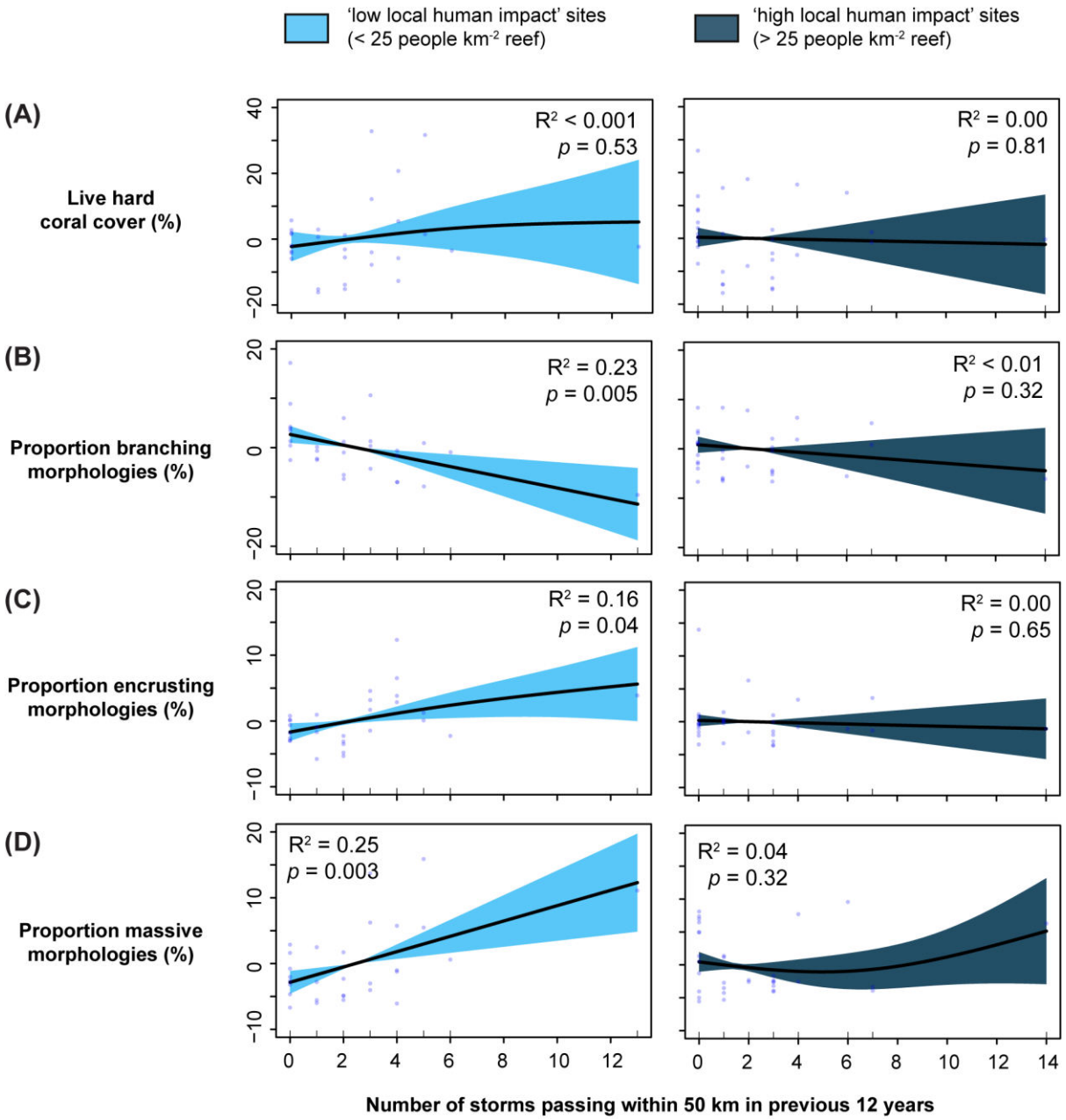


Figure 4 Smoother plots of normalised residuals from generalised additive models with 95% confidence intervals (shaded areas) to exemplify discrepancies in response-predictor relationships between local impact levels, using storm exposure as an example. The plots represent the explanatory power of storm exposure in predicting (**A**) live hard coral cover, and the proportion of (**B**) branching, (**C**) encrusting, and (**D**) massive morphologies, separated for sites with low *versus* high local impacts. Refer to Supplementary Figure 6 for all predictor-response plots from 'best-fit' models.

Individual relationships of 'best-fit' predictors for each response variable further emphasised discrepancies between benthic communities and environmental predictors driven by local human impacts (for all plots see Supplementary Figure 6). A clear example of this discrepancy can be seen in coral compositional changes with

increasing storm exposure. Whilst live hard coral cover remained unrelated to storm exposure under both local human impact levels (Figure 4A), the morphological composition was closely correlated with storm exposure at sites where local human impacts were low (Figure 4B–D). Specifically, with increasing storm exposure, the relative proportion of branching morphologies decreased significantly (Figure 4B), whereas encrusting (Figure 4C) and massive (Figure 4D) morphologies increased. No morphological changes with storm exposure were observed at sites with high local human impacts. Though these relationships appear primarily driven by few points at the higher end of storm exposure, they remained consistent when all reefs exposed to >10 storms were removed from the analysis – i.e. significant at 'low' impact sites (branching coral $p = 0.02$; encrusting coral $p = 0.02$; massive coral $p = 0.03$), insignificant at 'high' impact sites (all morphological growth forms $p > 0.05$), and no relationship for either impact for total live hard coral cover ($p > 0.05$).

4 Discussion

Under increasing climate change-associated stressors and local anthropogenic influence (Burke et al., 2011; Gattuso et al., 2015; IPCC, 2019), it is particularly important for researchers and planners to maximise the ability of models to predict ecosystem futures to allow appropriate mitigation strategies to be implemented. This study indicates that the role of local human impacts in changing coral reef ecological communities and their responses to environmental drivers should be accounted for. The results revealed that local human impacts influenced both benthic community structure and relationships with biophysical predictors. Specifically, models based on spatio-physical predictors (i.e. reef depth, latitude, storm exposure, and relief) exhibited high power at explaining benthic assemblages under low local human impacts but were strongly compromised where local human impacts were high. Importantly, these outcomes remained similar when our threshold for human impacts, informed by previous work, was reduced or increased in the frame of a sensitivity analysis. Increasing sewage input, agricultural run-off, and sedimentation are potential changes associated with increasing human densities that reduce water quality and affect benthic communities (Fabricius, 2005; Fabricius et al., 2005; Ford et al., 2017). Furthermore, as fishing removes biomass of functionally important fish species, important top-down control of some benthic organisms is lost (Bellwood et al., 2004). These localised human impacts may homogenise benthic communities by driving ecological reorganisation that favours tolerant taxa (Darling et al., 2019). Our results indicate that this homogenisation may be occurring at Pacific Island reefs that are exposed to local human impacts, leading to novel systems that react fundamentally differently and unpredictably to environmental predictors compared to reefs less influenced by humans (Williams et al., 2015a). In turn, we expect that local human impacts will influence responses of coral reefs to climate change-related stressors, and that reefs close to human populations will require context-specific management approaches to maximise their future sustainability and associated critical ecosystem services (Moberg and Folke, 1999).

The results emphasise the variation in benthic assemblages that exists among Pacific Island reefs exposed to different levels of local human impact. Benthic communities were not restricted to distinct regimes dominated by either hard corals

548 or macroalgae, supporting previous studies from the Pacific (Bruno et al., 2009;
549 Albert et al., 2012; Jouffray et al., 2015, 2019; Smith et al., 2016). In fact,
550 macroalgae was the least common of all the algal groups, with turf algae and CCA
551 more prominent on these outer reefs. Reefs at sites with higher local human impacts
552 comprised significantly more turf algae and less live hard coral. Abundant and
553 diverse outer reef coral communities (e.g. Ellis et al., 2017) have likely retained
554 sensitive species, facilitating measurable differences (i.e. reductions in live hard
555 coral cover) under higher local human impacts. Higher turf algae coverage at sites
556 with more local human impacts provides further evidence that turf algae may
557 become the dominant benthic group on degraded Pacific Island reefs (Jouffray et al.,
558 2015; Smith et al., 2016; Tebbett and Bellwood, 2019). This may contrast with coral
559 reef systems in the Caribbean, where macroalgae naturally play a more dominant
560 role (Roff and Mumby, 2012). Furthermore, a signal of local human impact may have
561 been detected if the data had distinguished macroalgae into fleshy/frondose and
562 calcified types (e.g. Smith et al., 2016; Cannon et al., 2019). A similar link between
563 human population size, hard coral cover, and turf algae has also recently been
564 reported from sites in the Indian Ocean (Brown et al., 2017).
565
566 The 'spatio-physical' models were weak in explaining the variance of benthic
567 communities exposed to relatively more local human impacts. At these sites, model
568 selection identified mostly local biotic controls or ecological features such as fish
569 biomass and market gravity to be of highest relative importance. These results
570 suggest that reefs altered by chronic local human impacts become decoupled from
571 spatio-physical factors (Williams et al., 2015a) and become more related to factors
572 associated with human activities (e.g. market gravity) or local ecological features
573 (e.g. biomass of functional groups of fish). Interestingly, this outcome contrasts to
574 recent findings by Robinson et al. (2018) who did not detect decoupling at inhabited
575 *versus* uninhabited reefs. Our different outcomes for decoupling could in part be
576 explained by Robinson et al. (2018) combining (i) hard corals and CCA, and (ii)
577 fleshy macroalgae and turf algae, each of which we found to exhibit different
578 responses to local impacts (i.e. with higher local impacts hard coral cover reduced
579 whereas CCA remained unchanged, turf algae increased whereas macroalgae
580 remained unchanged). Model selection indicated that the specific spatio-physical
581 predictors whose influence were most disrupted by local human impacts were storm
582 exposure and reef depth. Storms can have mixed effects, benefitting reefs by
583 alleviating thermal stress during warmer summer months but also causing physical
584 destruction, particularly to delicate branching coral morphologies, leading to a higher
585 proportion of more robust massive morphologies (Heron et al., 2005; Manzello et al.,
586 2007). Accordingly, when local human impacts were low, coral communities
587 comprised relatively less branching and more encrusting and massive morphologies
588 at sites subject to more frequent storms. However, relationships between storm
589 exposure and benthic assemblages were only observed at sites classified as having
590 low local human impacts. Returning to the concept that local human impacts drive
591 ecological reorganisation, we would expect reefs with less local human impacts to
592 harbour a great diversity of species and morphologies, thus allowing for greater
593 levels of ecological reorganisation in response to a stormier environment (i.e.
594 favouring more robust morphologies). We anticipate that Pacific reefs would more
595 likely display this phenomenon than Caribbean reefs due to a significantly larger
596 initial species pool, with greater response diversity and functional redundancy

affording a higher level of ecological insurance (Elmqvist et al., 2003; Bellwood et al., 2004; Nyström, 2006), and a loss of structurally-complex coral species throughout most of the Caribbean over past decades (Alvarez-Filip et al., 2009). It would be interesting to test whether storm exposure results in more conspicuous negative impacts on coral cover (e.g. Gardner et al., 2005) in less diverse regions due to the limited capacity for ecological reorganisation to a tolerant community, even in sites with minimal local human impact. In terms of reef depth, benthic communities at sites with low local human impacts also exhibited a higher level of depth-structuring (particularly in terms of coral cover and composition, consistent with Huston, 1985) compared to those with high local human impacts. Island relief was also identified as being a strong predictor of benthic community structure (despite being found to be a weak predictor on central-western Pacific reefs - Robinson et al., 2018), and interestingly this role was maintained regardless of local human impact level. Importantly, when considering latitude – collinear with DHW/cumulative thermal stress – as an individual predictor, our results neither contradict nor confirm previous observations that local impacts exacerbate the sensitivity of coral communities to thermal stress (Wiedenmann et al., 2013; Ellis et al., 2019), instead highlighting a large variance among sites.

Thermal stress and the intensity of storms are projected to increase under future climate change scenarios (IPCC, 2019), with profound implications for coral reefs and adjacent ecosystems. Our findings suggest that while the effects of factors associated with climate change (e.g. storm exposure) on Pacific reef benthic assemblages may be reasonably well-predicted where local impacts are low, system responses become less predictable as local human impacts increase. In both marine and terrestrial systems, structural changes caused by local impacts have profoundly changed how ecosystems respond to natural stressors: for example, local stressors have affected how parts of Australia's Great Barrier Reef have recovered from recent climate change impacts (MacNeil et al., 2019; Mellin et al., 2019) and habitat fragmentation and modification have exacerbated recent impacts of tropical and temperate forest fires (Brando et al., 2014; Alencar et al., 2015; Taylor et al., 2016). Because the effects of storms are strongly dependent not only on their intensity, but also the extent of the fetch, their frequency, and intrinsic reef properties such as topography (Lugo et al., 2000; Heron et al., 2005), this study incorporated all recorded storms (category 1–5 on the Saffir-Simpson Hurricane Scale) passing within 50 km of each site. We thus cannot deduce benthic community responses to increasing storm *intensity*, which is projected to occur (IPCC, 2019).

Functional groups of herbivorous fishes also emerged to be of contrasting relative importance depending on the level of local human impact, shifting from scrapers and small excavators at less impacted reefs to grazers at more impacted reefs. Browsers were of similar importance at reefs exposed to both local human impact levels, perhaps linked to the fact that their food source (macroalgae) remained constant regardless of local human impact level. Additional reasons for this could be that browsers have remained more resilient to fishing pressure than other herbivores, or that visual survey data does not accurately represent browser populations (for example some browser species are known to be particularly wary of divers – Kulbicki, 1998). Fish that act on turf algae and/or on surfaces available for coral settlement seem to be more sensitive to local human impacts, likely in response to

benthic community shifts. Scrapers and small excavators clear substrate for calcifiers, justifying their higher relative importance in models focused on less locally impacted reefs where live hard coral cover was higher and conditions for settlement and growth of juvenile corals were likely better (e.g. less nutrients, lower sedimentation). Contrastingly, grazers crop and maintain algal turfs, explaining their importance under higher local human impacts where turf algae were more dominant. These results align with findings in the Hawaiian Archipelago, where biomass of grazers and scrapers were the most important predictors of turf/macroalgal, and calcified regimes, respectively (Jouffray et al., 2015; see also Robinson et al., 2018). Though collinearity tests ruled out significant, potentially confounding relationships between biomass of different functional groups with individual abiotic predictors, it is important to acknowledge that fish communities themselves can be affected by various physical predictors (Williams et al., 2015b; Samoilys et al., 2019), which could in turn influence benthic structure.

Other factors not included in these analyses are known to structure benthic assemblages, including chlorophyll, SSTs, and wave exposure (Gove et al., 2013, 2015; Williams et al., 2013; Robinson et al., 2018; Darling et al., 2019). Remotely sensed chlorophyll data captures offshore productivity, but we expected land-based input to dominate many of these reefs which are close to land, while the survey design (sometimes around the periphery of small islands/atolls) made wave exposure challenging to quantify. Additionally, wave exposure, mean SSTs, and climatological ranges can be relatively well-captured by latitude in the Pacific (Gove et al., 2013). Also, although this study goes into more detail than many similar large-scale analyses by evaluating coral growth forms, it is still limited in its ability to quantify ecological reorganisation, which would require higher resolution data (at least family or genus). This limitation can be overcome by broad-scale surveys refining the level at which hard coral communities are recorded, which will become easier with improvements in automated software tools. These results do however emphasise that even broad morphological groupings (i.e. branching, massive, encrusting morphologies) provide pertinent information on ecological changes and can improve model performance compared to when overall hard coral cover is considered (Gove et al., 2015).

Importantly, the threshold used in this study for determining low and high impact, while informed by a previous study, was set *a priori* and thus does not allow defining a 'carrying capacity' of human density – this would require a different survey design and analytical approach, and should be pursued in future studies. We would however suggest that although this metric is most applicable to areas where customary resource use is common practice, we anticipate that this threshold (25 humans km^{-2} reef) is highly relevant across the Pacific region (i.e. given that it is a median point in this dataset for which sites were selected due to being regionally representative of fished areas). Furthermore, the study design was not originally meant to address macroecological questions but was nonetheless the best available to study the questions we were interested in (with incorporation of appropriate secondary data on local environmental context). Again, future studies should address this by appropriate designs that allow for large-scale comparability and collect both ecological and socio-economic local data. Our findings indicate that island relief is a factor that should be considered in designing regional sampling

programs with comparable sites. Finally, we should aim to obtain context-specific information on factors associated with human population density (e.g. sewage treatment presence, farming and associated fertiliser-usage) that strengthens our ability to predict benthic communities under various levels of human population density and improve its use as a proxy of local human impact.

Our findings contribute to a better understanding of the role of local human impacts on diverse ecosystems such as tropical coral reefs. The results provide empirical evidence that local human impacts drive conspicuous changes in benthic community relationships with environmental predictors, with indications of ecological reorganisation. Even if decisive steps are taken to reduce fossil fuel emissions, most reefs will suffer long-term degradation from the effects of climate change by 2050, and >75% of reefs will experience annual severe bleaching (Frieler et al., 2013; van Hooidonk et al., 2016). Our results show that local human impacts can lead to increasingly unpredictable relationships between benthic communities and their physical environment, and that overlooking their role could pave way to significant errors in future projections, potentially compromising mitigation efforts.

5 Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

6 Author Contributions

AF developed the study idea with close support from JBJ, AN, BM and SF. AF led the statistical analyses together with input from JBJ, GW and SF. BM and FM provided expertise on the original data. All authors provided support throughout the interpretation of the results and development of the manuscript. All authors approve this final version.

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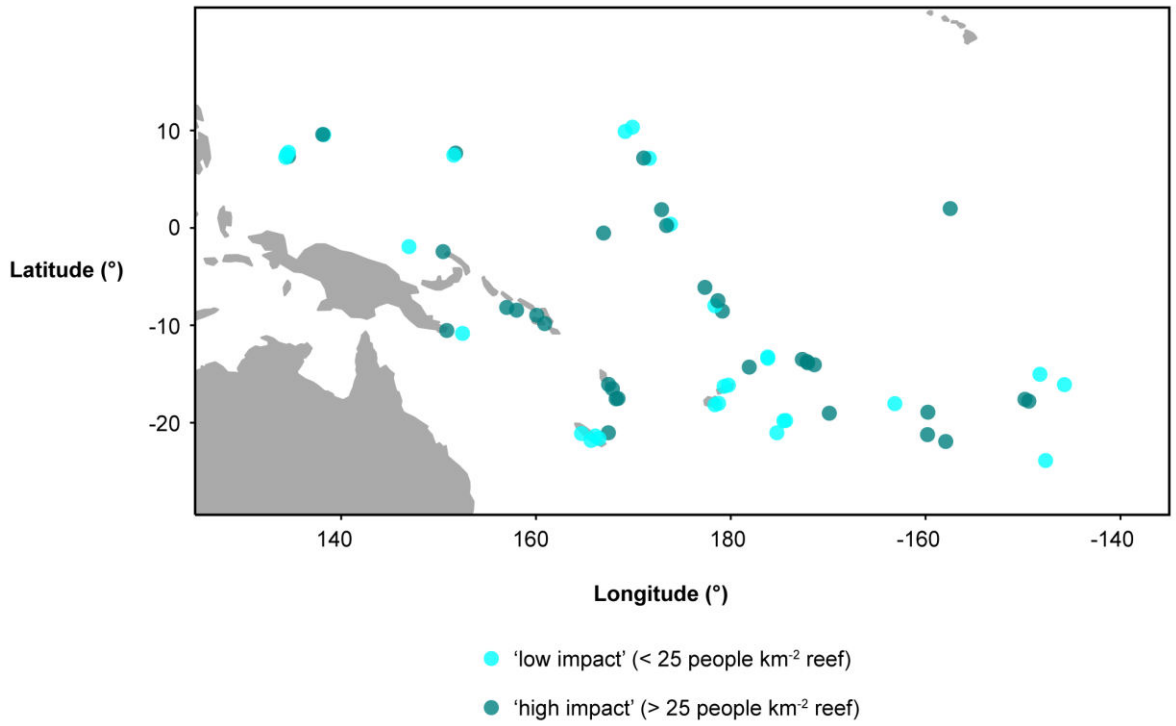
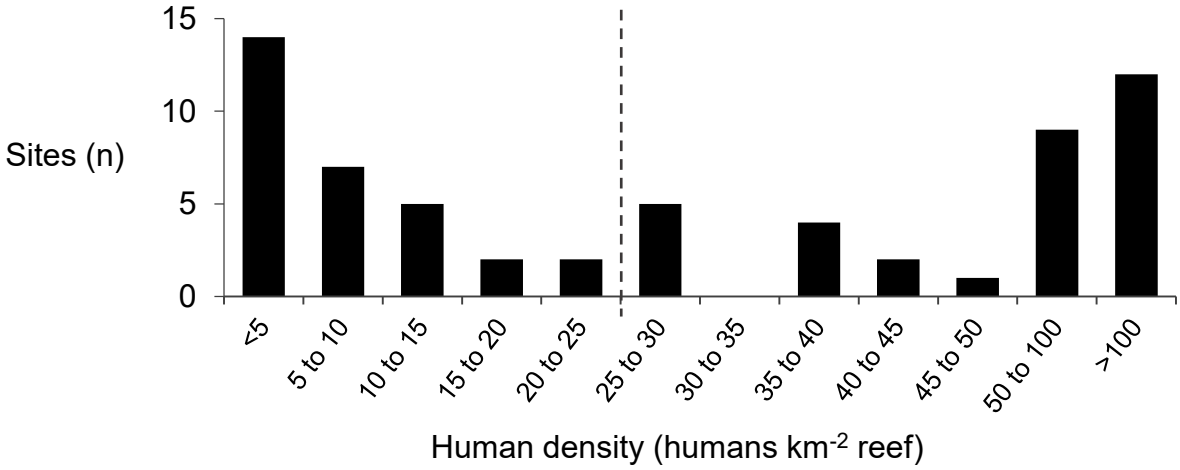
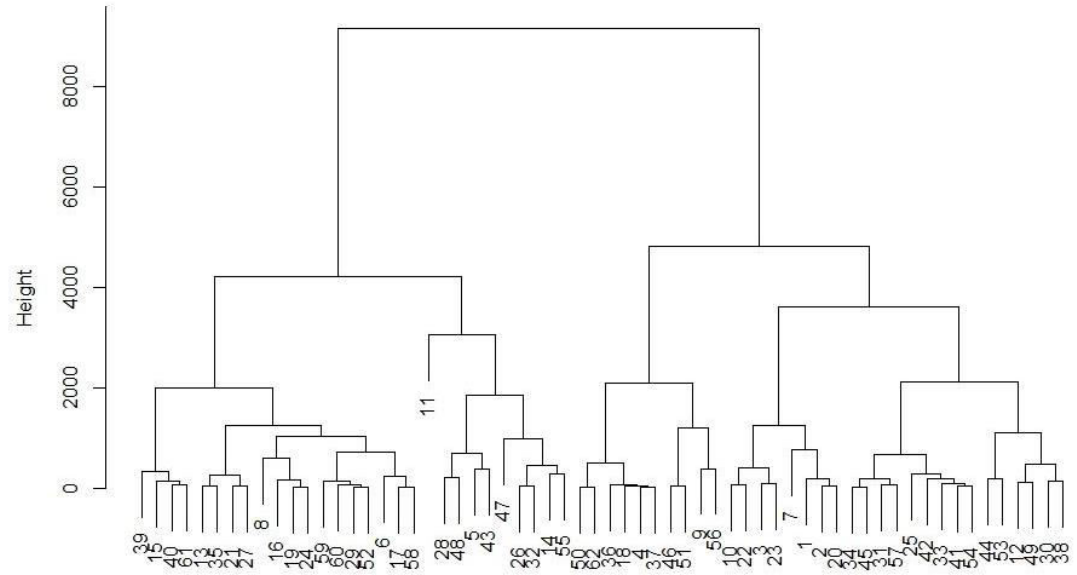


Supplementary Figure 1 - Map of the 62 sites surveyed across 17 different Pacific Island countries and territories, coloured by local impact level.

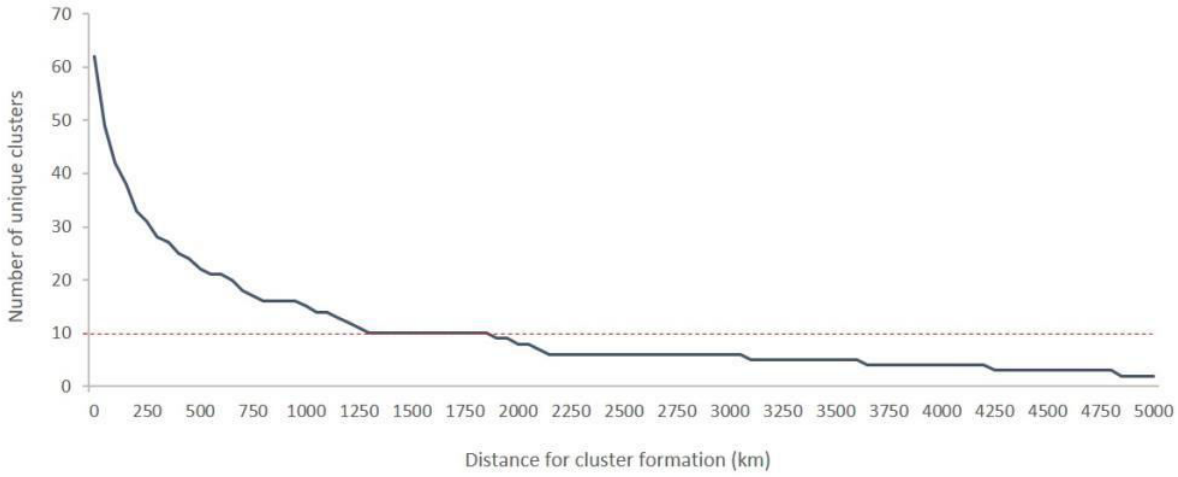


Supplementary Figure 2 - Number of sites by human density (humans km^{-2} reef). Dashed line indicates threshold separating low impact from high impact sites.

(A)

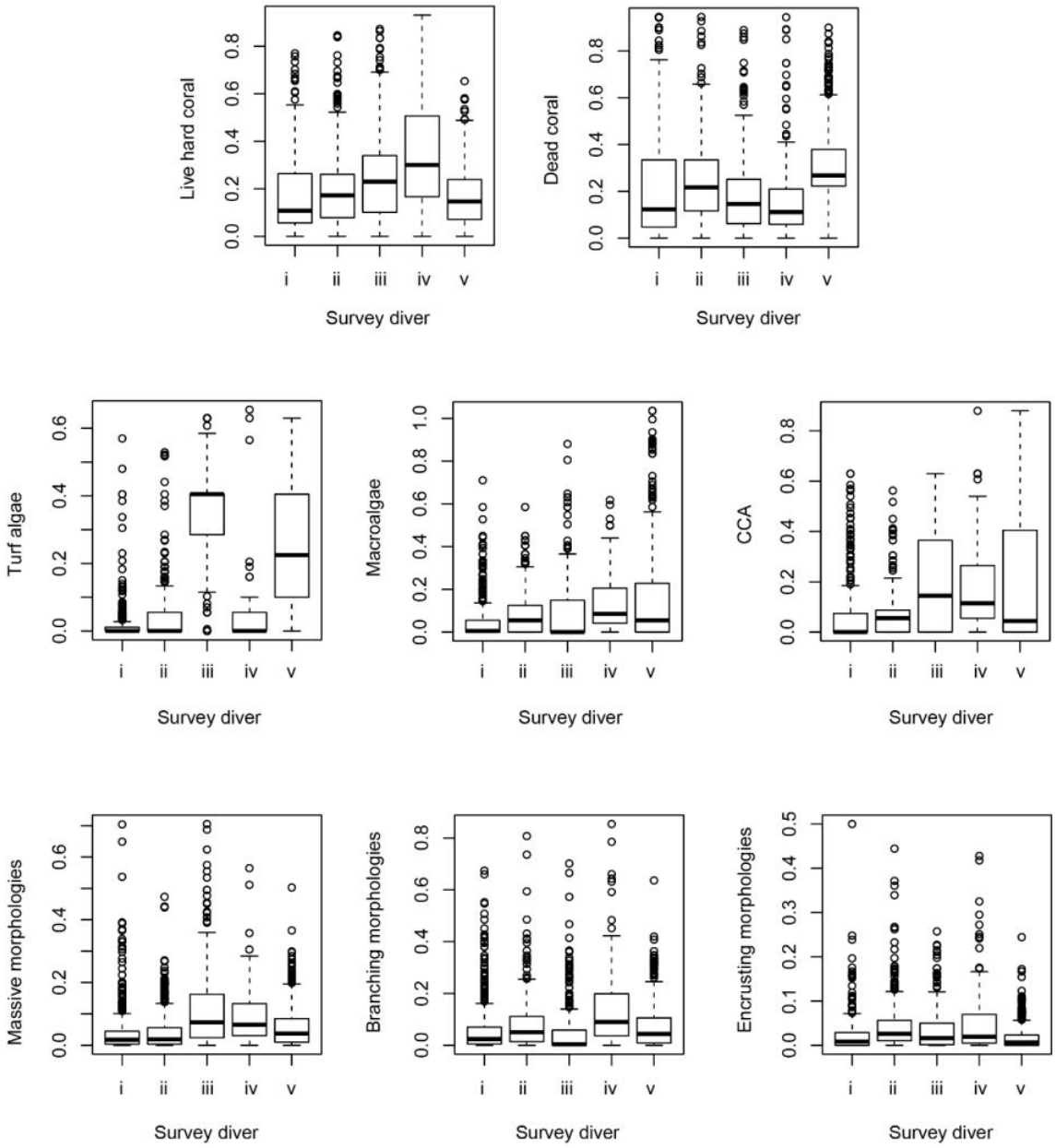


(B)



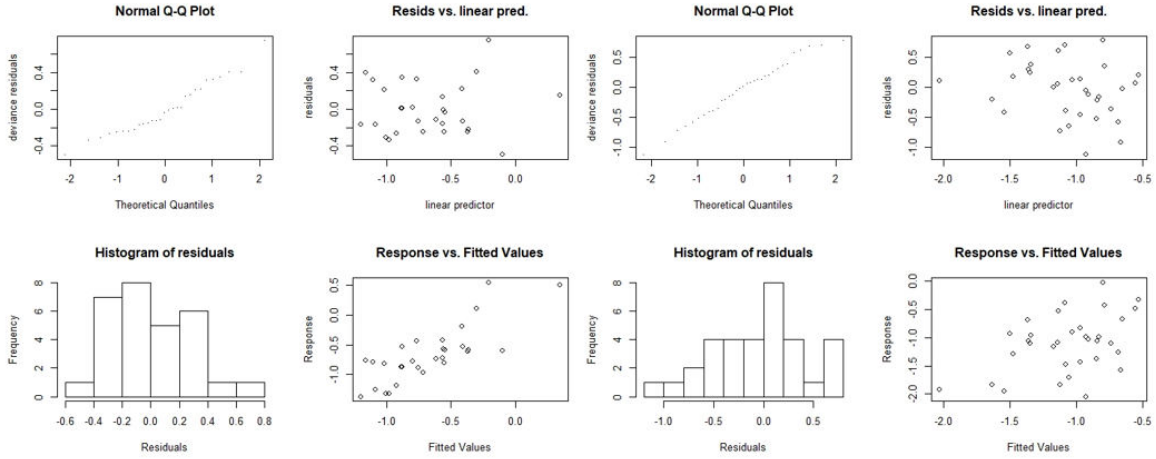
Supplementary Figure 3 - To account for possible spatial autocorrelation among sites, we included island cluster as a random effect within models (based on methodology of Williams et al. 2015*). Island clusters were identified using (A) hierarchical clustering based on pairwise Euclidean distances between each of the 62 sites, by finding (B) an inflection point in the number of unique clusters and cluster distance which we identified to be at ~1300 km, resulting in ten unique island clusters.

*Williams GJ, Gove JM, Eynaud Y, Zgliczynski BJ, Sandin SA. (2015) Local human impacts decouple natural biophysical relationships on Pacific coral reefs. *Ecography*, **38**, 751–761.

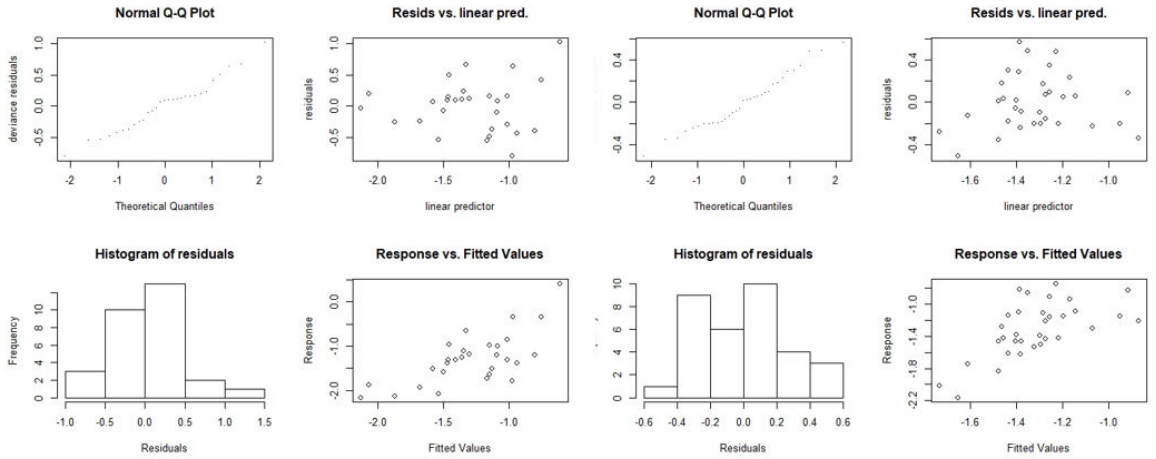


Supplementary Figure 4 - Boxplots representing ranges of response variables recorded by the core survey diver team - the core survey team consisted of five divers, who recorded 94% of all transects. Additional surveyors were included in the remaining 6%. As surveyor bias is inherent to such datasets, we tested for surveyor effects on our response variables. These tests indicated that significantly higher turf algae coverage was reported by two of the core survey team (survey divers iii and v). It became apparent that even within one reef, there were discrepancies in the reported turf algae cover between these survey divers and survey divers i, ii, and iv. This was not an issue with other benthic groups nor morphological classifications of hard corals (i.e. massive, branching, and encrusting). To account for the differences in turf algae reporting, we scored the contribution of survey divers iii and v to total surveys at each reef on a continuous scale from 0 to 1 (i.e. 0 meaning survey divers iii and v were not present on any transects at the reef, and 1 meaning all transects at a reef were conducted by survey diver iii and/or v). This score (referred to as *bias_score*) was included as a random effect in subsequent turf algae-focused models.

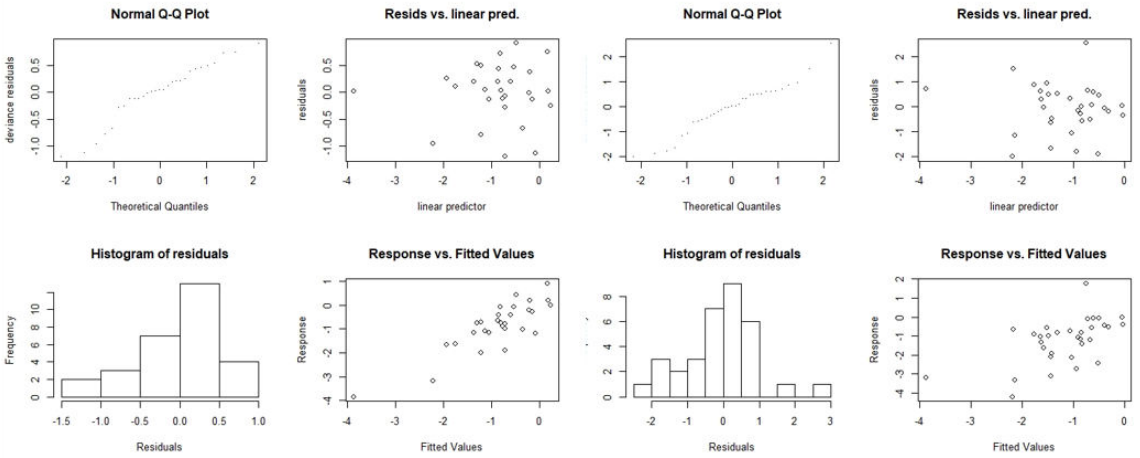
Live hard coral



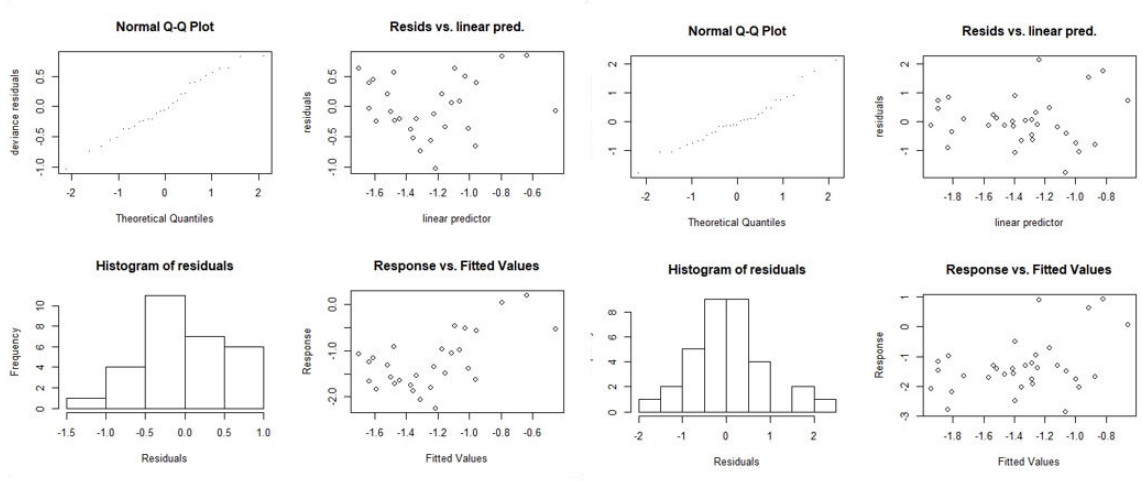
Dead hard coral



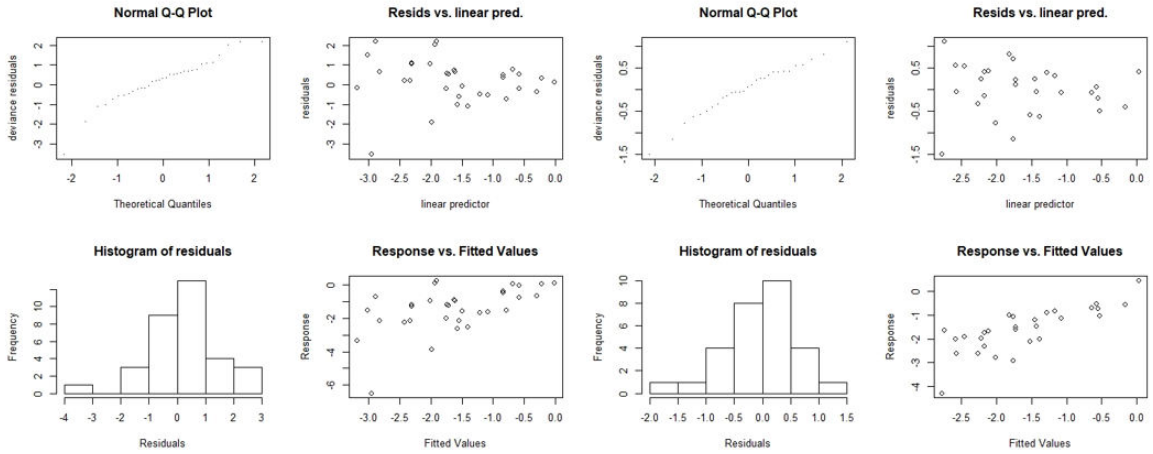
Branching morphologies



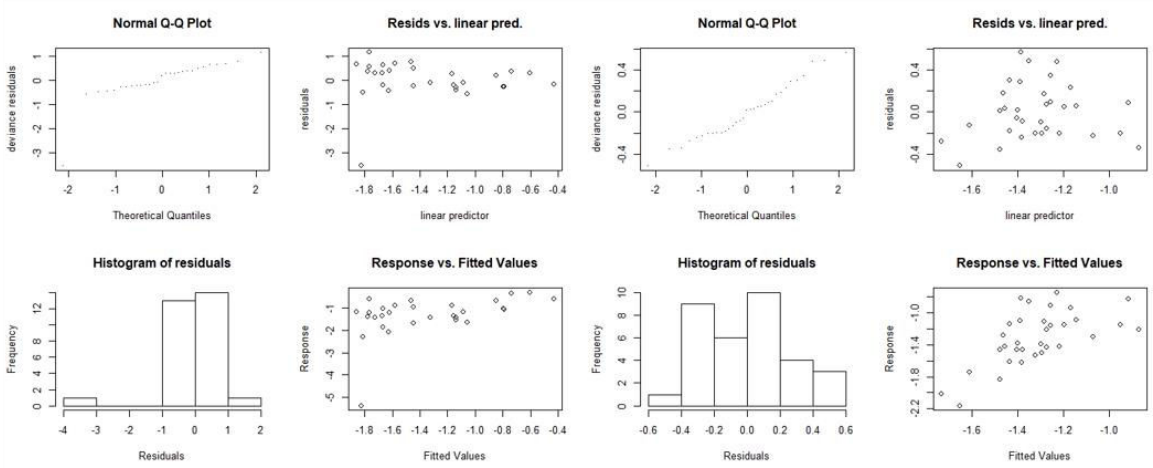
Encrusting morphologies



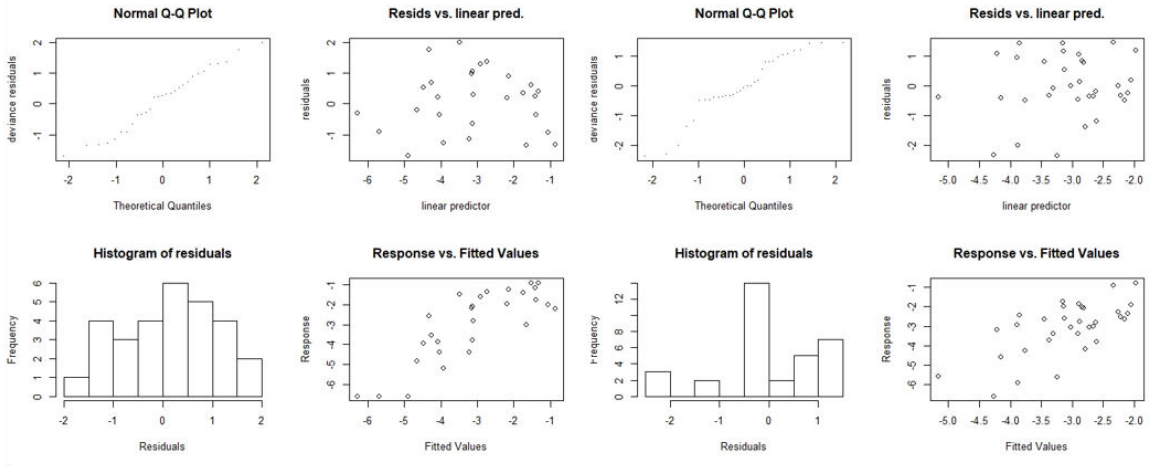
Massive morphologies



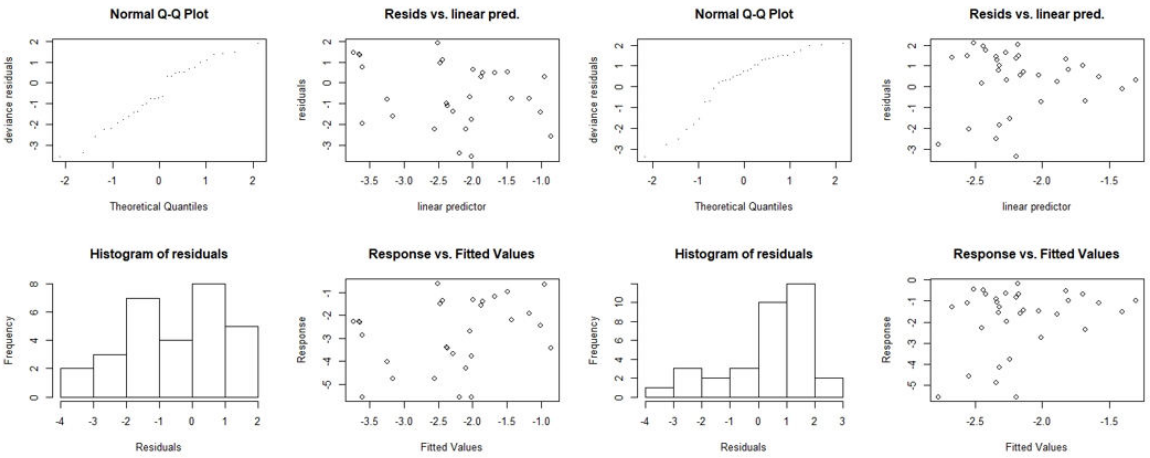
CCA



Fleshy algae

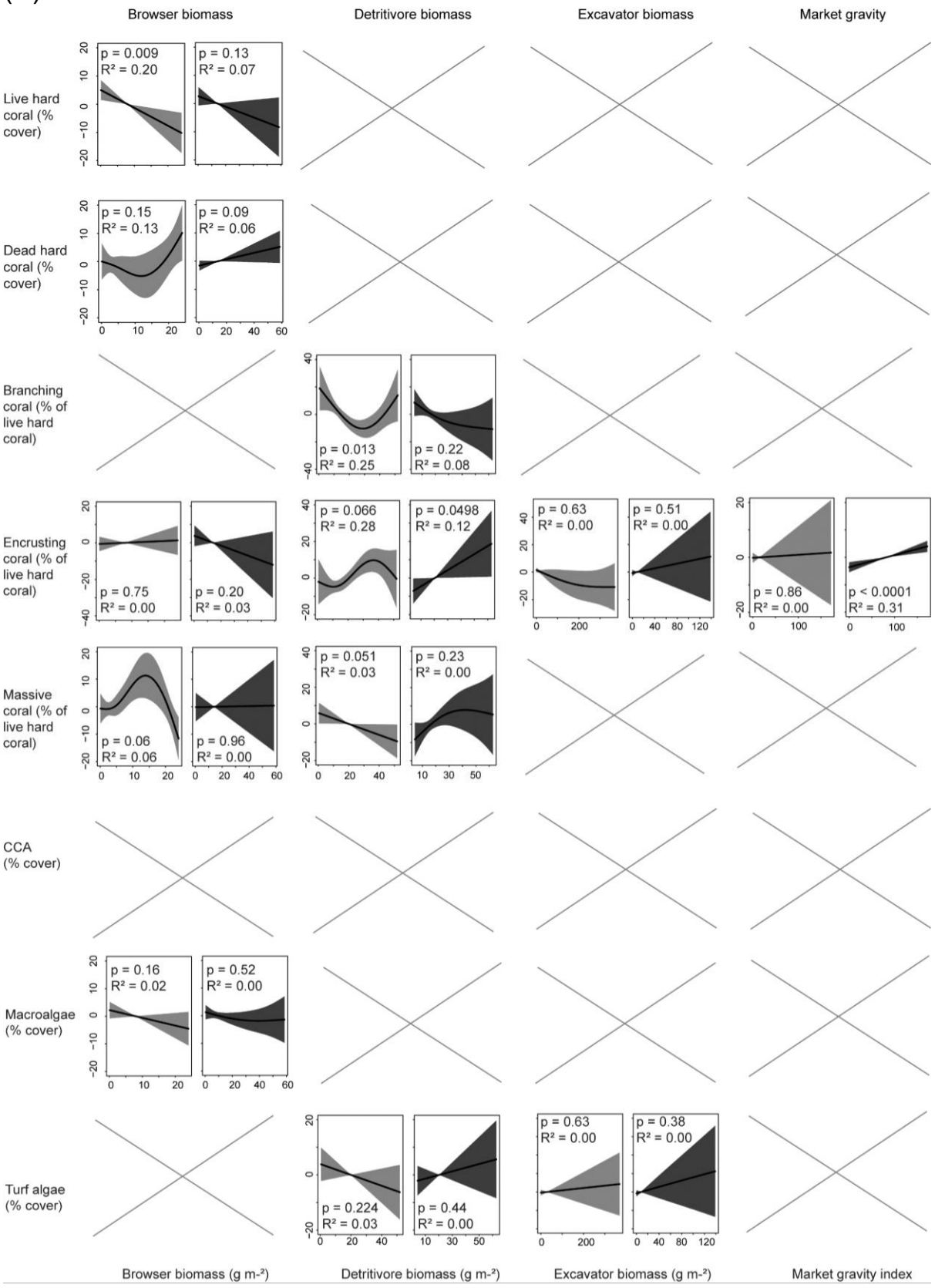


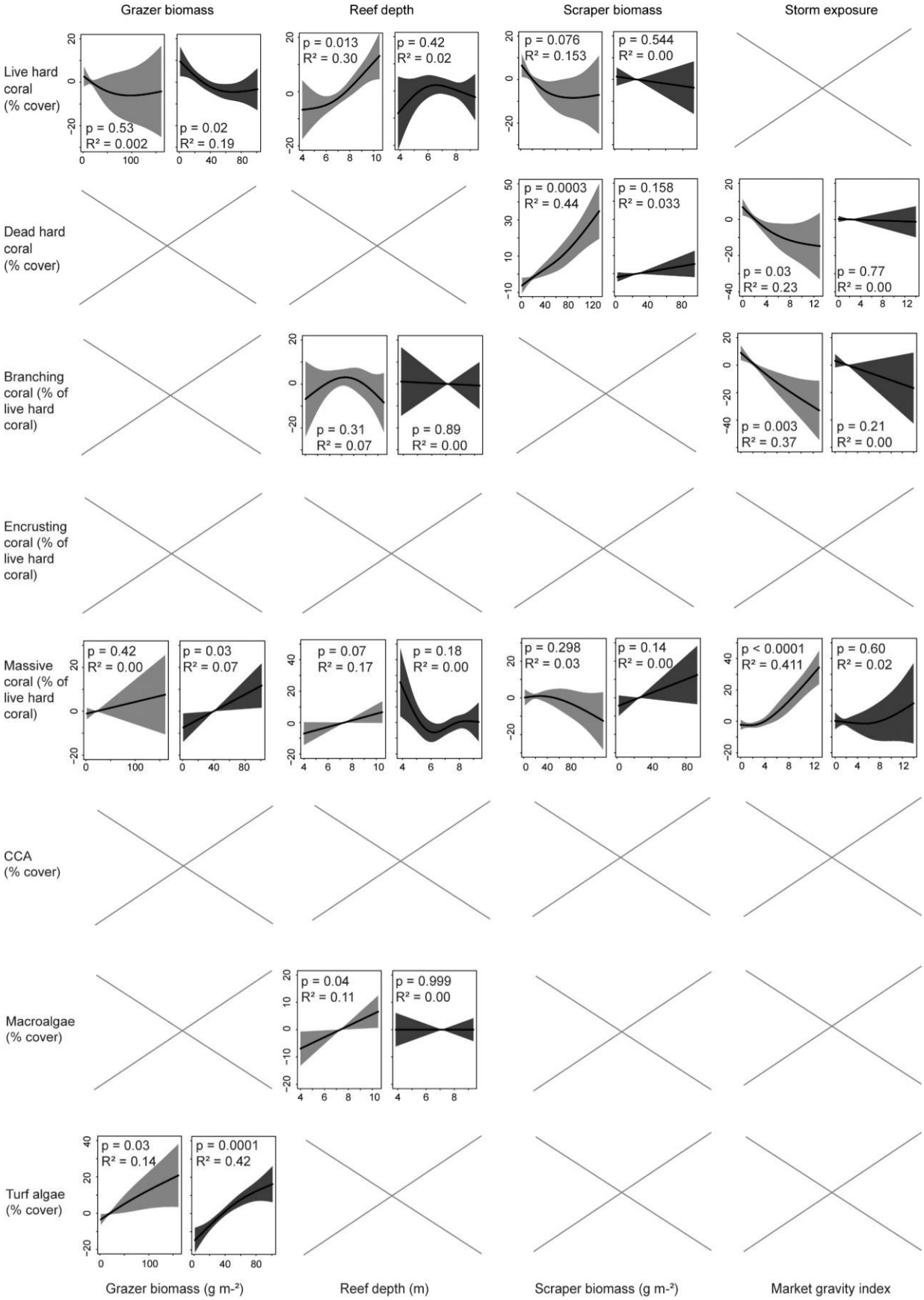
Turf algae



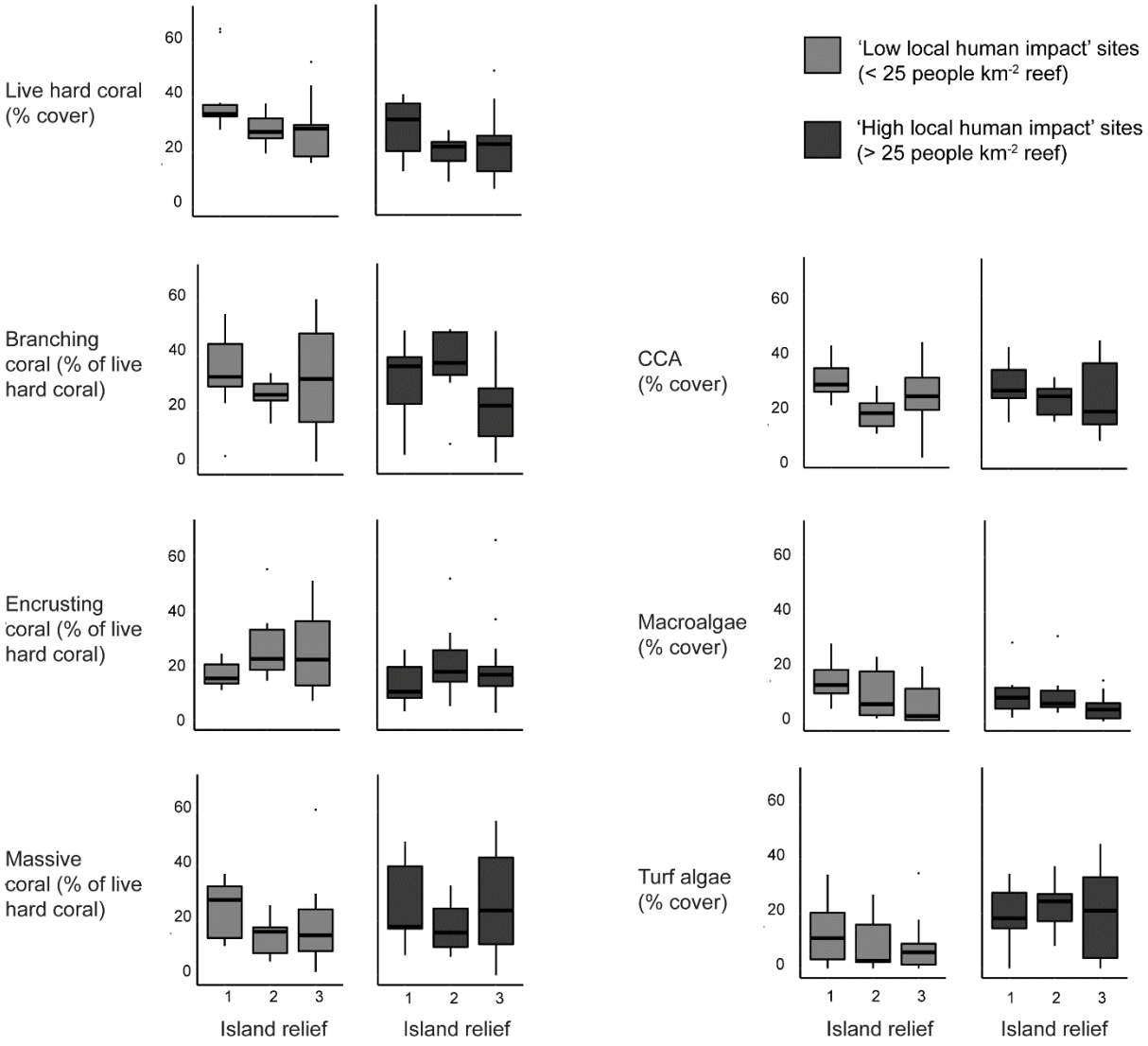
Supplementary Figure 5 - Residuals ($gam.check) of 'spatio-physical' models (for each response variable (in order from top to bottom: live hard coral, dead hard coral, branching morphologies, encrusting morphologies, massive morphologies, CCA, macroalgae, turf algae). Left set of graphs = models based on low local impact sites (< 25 humans km^{-2} reef); right set of graphs = models based on high local impact reefs (> 25 humans km^{-2} reef):

(A)


Browser biomass
Detritivore biomass
Excavator biomass
Market gravity
Live hard coral (% cover)
p = 0.009
R² = 0.20
p = 0.13
R² = 0.07
Dead hard coral (% cover)
p = 0.15
R² = 0.13
p = 0.09
R² = 0.06
Branching coral (% of live hard coral)
p = 0.013
R² = 0.25
p = 0.22
R² = 0.08
Encrusting coral (% of live hard coral)
p = 0.75
R² = 0.00
p = 0.20
R² = 0.03
p = 0.066
R² = 0.28
p = 0.0498
R² = 0.12
p = 0.63
R² = 0.00
p = 0.51
R² = 0.00
p = 0.86
R² = 0.00
p < 0.0001
R² = 0.31
Massive coral (% of live hard coral)
p = 0.06
R² = 0.06
p = 0.96
R² = 0.00
p = 0.051
R² = 0.03
p = 0.23
R² = 0.00
CCA (% cover)
Macroalgae (% cover)
p = 0.16
R² = 0.02
p = 0.52
R² = 0.00
Turf algae (% cover)
p = 0.224
R² = 0.03
p = 0.44
R² = 0.00
p = 0.63
R² = 0.00
p = 0.38
R² = 0.00
Browser biomass (g m-²)
Detritivore biomass (g m-²)
Excavator biomass (g m-²)
Market gravity index


Grazer biomass
Reef depth
Scraper biomass
Storm exposure
Live hard coral (% cover)
p = 0.53 R² = 0.002
p = 0.02 R² = 0.19
p = 0.013 R² = 0.30
p = 0.42 R² = 0.02
p = 0.076 R² = 0.153
p = 0.544 R² = 0.00
Dead hard coral (% cover)
p = 0.0003 R² = 0.44
p = 0.158 R² = 0.033
p = 0.03 R² = 0.23
p = 0.77 R² = 0.00
Branching coral (% of live hard coral)
p = 0.31 R² = 0.07
p = 0.89 R² = 0.00
p = 0.003 R² = 0.37
p = 0.21 R² = 0.00
Encrusting coral (% of live hard coral)
Massive coral (% of live hard coral)
p = 0.42 R² = 0.00
p = 0.03 R² = 0.07
p = 0.07 R² = 0.17
p = 0.18 R² = 0.00
p = 0.298 R² = 0.03
p = 0.14 R² = 0.00
p < 0.0001 R² = 0.411
p = 0.60 R² = 0.02
CCA (% cover)
Macroalgae (% cover)
p = 0.04 R² = 0.11
p = 0.999 R² = 0.00
Turf algae (% cover)
p = 0.03 R² = 0.14
p = 0.0001 R² = 0.42
Grazer biomass (g m-²)
Reef depth (m)
Scraper biomass (g m-²)
Market gravity index

(B)



Supplementary Figure 6 – Individual relationships between selected predictors for each respective response variables as per 'best-fit' model outcomes. (A) Smoother plots of normalised residuals from generalised additive mixed effect models (*gamm4* package) with 95% confidence intervals (shaded areas). Plots are based on the $gam output from these models. These graphs provide relationships between individual response variables and predictors that were selected for 'best-fit' models (those with Akaike weight > 0.05; see Figure 4; Supplementary Table 4) at outer reef sites with low and/or high local human impacts. Plots are provided in terms of reefs exposed to low (light grey/left panel) *versus* high (dark grey/right panel) local impact as determined using a threshold of 25 humans km^{-2} reef. Large crosses (X) mean that the predictor was not selected for 'best-fit' models for reefs exposed to either impact level. (B) Boxplots conveying relationships between the predictor island relief and benthic response variables for which it was selected for 'best-fit' models (i.e. those with Akaike weight > 0.05; see Figure 4; Supplementary Table 4).

Supplementary Table 1 - Table containing survey dates and timelines of disturbances (up to 12 years before surveys) with associated references provided.

**Additional survey information: Criteria for site selection: (i) having active reef fisheries, (ii) being representative of the country, (iii) being relatively closed systems, (iv) being appropriate in size, (v) possessing diverse habitats*, (vi) presenting no major logistical problems, (vii) having been previously investigated and (viii) presenting particular interest for the respective Fisheries Agency. For full details see Pinca et al. (2010). Originals surveys grouped reefs into four geomorphological structures, but this study focused only on outer (fore-) reefs (primarily due to replication). Though 63 individual outer reefs were surveyed, one reef had less than three replicate transects and thus was removed, leaving 62 replicate reefs.*

Country	Sites & Survey Dates	History of Events	References
Cook Islands	Aitutaki, Feb-2007 Mangaia Oct-2007 Palmerston Feb-2007 Rarotonga Oct-2007	1997: Several cyclones (including Cyclone Martin – category 3) 2000: Mass bleaching event (up to 80% *Acropora* bleached in Rarotonga) 2002/2003: Major cyclone 2003/2004: Major cyclone 2004/2005: Several destructive cyclones (six)	Lovell 2001, Cumming et al. 2002, Salvat 2002, de Scally 2008, Pinca et al. 2009a
Fiji	Dromuna Apr-2003 Lakeba Jun-2003 Mali Jun-2003 Muiavuso Apr-2003	2000: Mass bleaching event (40–80% coral mortality) 2001: Minor bleaching 2002: Bleaching in shallow areas	Goreau et al. 2000, Cumming et al. 2002, Lovell et al. 2004, Friedman et al. 2010
French Polynesia	Fakarava Mar-2004 Maatea May-2006 Mataiea May/Jun-2003 Raivavae Mar-2004 Tikehau Oct-2003	1994: Major bleaching but low mortality 1997: Cyclone Martin hit (southern) French Polynesia. Patchy bleaching and mortality 2002: Start of COTS outbreak (at Society Archipelago and Australes)	Salvat 2002, Vieux et al. 2004, Adjeroud et al. 2005, Kronen et al. 2008a, Trapon et al. 2011

FSM	Piis-Panewu Apr-2006 Riiken Apr-2006 Romanum Apr-2006 Yyin May-2006	2005: Concerning levels of COTs reported from rapid assessment	George et al. 2008, Kronen et al. 2009a
Kiribati	Abaiang Jun-2004 Abemama May-2004 Kiritimati Sep-2004 Kuria May-2004	2003: Fish kill in atolls of Gilbert Islands 2004: (post survey) first mass bleaching event internationally reported	Awira et al. 2008, Donner et al. 2010
Marshall Islands	Ailuk Aug-2007 Arno Sep-2007 Laura Sep-2007 Likiep Aug-2007	2001: Bleaching mortality observed (particularly shallow *Acropora*) 2003: Bleaching event, high incidence of *Acropora* white disease 2004: Elevated COTS (>1000 km^{-2}) found in Majuro's SW lagoon, with associated coral mortality 2006: Storm caused large surf and storm surge (become Typhoon Soulik) – *Acropora* colonies damaged. Also bleaching event with up to 90% *Acropora* bleaching (20–50% mortality) in lagoons.	Beger et al. 2008 Pinca et al. 2009b
Nauru	Nauru Oct-2005	2000: Phosphate reserves are virtually exhausted (80% of the island's surface has been strip mined – mining started in 1908) 2002: High rainfall and some bleaching 2003: Coral bleaching and mass fish kills both linked to elevated SSTs, strong upwelling or drops in dissolved oxygen levels. 2004: Large number of	Sulu et al. 2002, Lovell et al. 2004, Sauni et al. 2007, Chin et al. 2011

		seabirds found dead without a known cause	
New Caledonia	Luengoni Jun-2004 Moindou May-2004 Ouasse Aug-2004 Oundjo Feb-2004 Thio Mar-2004	1998 and 2001: Extensive coral loss due to COTs, bleaching and disease 2003: Cyclone (Erica) led to 10–80% coral loss	Sulu et al. 2002, Lovell et al. 2004, Kronen et al. 2009b
Niue	All Niue May-2005	2004: Major cyclone (Cyclone Heta – category 5) caused 20–90% reefs on the western coast to be flattened, hence live coral in surveys sometimes <2%	Vieux et al. 2004, Kronen et al. 2008b, Chin et al. 2011
Palau	Airai Apr-2007 Koror May-2007 Ngarchelong Apr-2007 Ngatpang Apr-2007	1998: Mass bleaching from El Niño reduced coral cover from 50–70% to 14–23% (exposed barrier reefs suffered more than coastal reefs). High mortality of soft corals. *Area is not exposed to cyclones and COTs outbreaks remain local events*	Friedman et al. 2009a, Golbuu 2011
Papua New Guinea	Andra Aug-2006 Panapompom Nov-2006 Sideia Oct-2006 Tsoilaunung Aug-2006	1996: Mass bleaching event (>50% corals at some sites) 1998: Mass bleaching from El Niño (75% *Acropora* affected at Kimbe Bay) 1999: Bleaching event 2000/2001: Mass bleaching event (>50% corals at some sites)	Lovell 2001, Cumming et al. 2002, Foale 2006, Friedman et al. 2009b
Samoa	Manono-uta Jun-2005 Salelavalu Aug-2005 Vailoa Jun-2005 Vaisala Aug-2005	2004: Cyclone (Heta – category 5) damaged 13% of coral reefs	Sulu et al. 2002, Lovell et al. 2004, Vunisea et al. 2008, Chin et al. 2011

Solomon Islands	Chubikopi Dec-2006 Marau Jun-2006 Nggela Jun-2006 Rarumana Aug-2006	2000: Mass bleaching 2002: Major cyclone (Zoe – category 5)	Lovell 2001, Cumming et al. 2002, Sulu et al. 2002, Pinca et al. 2009c
Tonga	Ha'afutu2 Sep-2008 Koulo Oct-2008 Lofanga Oct-2008 Manuka Sep-2008	1997: Cyclone (Hina – category 3) 1999: Cyclone (Cora – category 3) 2000: Cyclone (Mona – category 3), mass bleaching (up to 90% of *Goniastrea* and *Platygyra* colonies bleached)	Lovell 2001, Salvat 2002, Friedman et al. 2009c
Tuvalu	Funafuti Nov-2004 Niutao Apr-2005 Nukufetau Oct/Nov-2004 Vaitipu Mar/Apr-2005	1997: Major cyclones (Oliwa and Keli) 2002: Mass bleaching (30–40% corals bleached)	Sulu et al. 2002, Lovell et al. 2004, Sauni et al. 2008
Vanuatu	Maskelynes Nov/Dec-2003 Moso Jul-2003 Paunangisu Jul-2003 Uri-Uripiv Nov/Dec-2003	2001: Bleaching event (documented in Moso but lack of monitoring data for other areas)	Sulu et al. 2002, Friedman et al. 2008
Wallis and Futuna	All Futuna Nov-2005 Halalo Sep-2005 Vailala Sep-2005		Kronen et al. 2008c

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Supplementary Table 2 - Herbivorous fish recorded within surveys, classified into functional groups as specified in Heenan et al. (2016).

Functional group	**Species**
Browsers	*Calotomus carolinus*
Browsers	*Calotomus spinidens*
Browsers	*Kyphosus cinerascens*
Browsers	*Kyphosus* sp.
Browsers	*Kyphosus vaigiensis*
Browsers	*Leptoscarus vaigiensis*
Browsers	*Naso annulatus*[1]
Browsers	*Naso brachycentron*
Browsers	*Naso brevirostris*[1]
Browsers	*Naso lituratus*
Browsers	*Naso* sp.
Browsers	*Naso tuberosus*
Browsers	*Naso unicornis*
Browsers	*Platax orbicularis*
Browsers	*Platax* sp.
Browsers	*Platax teira*
Browsers	*Siganus canaliculatus*
Detritivores	*Ctenochaetus binotatus*
Detritivores	*Ctenochaetus cyanocheilus*
Detritivores	*Ctenochaetus flavicauda*
Detritivores	*Ctenochaetus hawaiiensis*
Detritivores	*Ctenochaetus marginatus*
Detritivores	*Ctenochaetus* sp.
Detritivores	*Ctenochaetus striatus*
Detritivores	*Ctenochaetus strigosus*
Detritivores	*Ctenochaetus tominiensis*
Grazers	*Acanthurus achilles*
Grazers	*Acanthurus auranticavus*
Grazers	*Acanthurus blochii*
Grazers	*Acanthurus dussumieri*
Grazers	*Acanthurus fowleri*
Grazers	*Acanthurus guttatus*
Grazers	*Acanthurus leucocheilus*
Grazers	*Acanthurus leucopareius*
Grazers	*Acanthurus lineatus*
Grazers	*Acanthurus maculiceps*
Grazers	*Acanthurus nigricans*
Grazers	*Acanthurus nigricauda*
Grazers	*Acanthurus nigrofuscus*
Grazers	*Acanthurus nigroris*
Grazers	*Acanthurus olivaceus*
Grazers	*Acanthurus pyroferus*
Grazers	*Acanthurus* sp.

Functional group	**Species**
Grazers	*Acanthurus triostegus*
Grazers	*Acanthurus xanthopterus*
Grazers	*Centropyge bicolor*
Grazers	*Centropyge bispinosa*
Grazers	*Centropyge flavissima*
Grazers	*Centropyge loricula*
Grazers	*Centropyge* sp.
Grazers	*Centropyge tibicen*
Grazers	*Centropyge vrolikii*
Grazers	*Siganus argenteus*
Grazers	*Siganus corallinus*
Grazers	*Siganus doliatus*
Grazers	*Siganus fuscescens*
Grazers	*Siganus guttatus*
Grazers	*Siganus lineatus*
Grazers	*Siganus niger*
Grazers	*Siganus puellus*
Grazers	*Siganus punctatissimus*
Grazers	*Siganus punctatus*
Grazers	*Siganus randalli*
Grazers	*Siganus* sp.
Grazers	*Siganus spinus*
Grazers	*Siganus stellatus*
Grazers	*Siganus uspi*
Grazers	*Siganus vermiculatus*
Grazers	*Siganus vulpinus*
Grazers	*Zebrasoma flavescens*
Grazers	*Zebrasoma rostratum*
Grazers	*Zebrasoma scopas*
Grazers	*Zebrasoma velifer*
Scrapers / small excavators	*Chlorurus bleekeri*
Scrapers / small excavators	*Chlorurus bowersi*
Scrapers / small excavators	*Chlorurus japanensis*
Scrapers / small excavators	*Chlorurus sordidus*
Scrapers / small excavators	*Chlorurus* sp.
Scrapers / small excavators	*Hipposcarus longiceps*
Scrapers / small excavators	*Scarus altipinnis*
Scrapers / small excavators	*Scarus chameleon*
Scrapers / small excavators	*Scarus dimidiatus*
Scrapers / small excavators	*Scarus festivus*
Scrapers / small excavators	*Scarus flavipectoralis*
Scrapers / small excavators	*Scarus forsteni*
Scrapers / small excavators	*Scarus frenatus*
Scrapers / small excavators	*Scarus ghobban*
Scrapers / small excavators	*Scarus globiceps*
Scrapers / small excavators	*Scarus hypselopterus*

Functional group	**Species**
Scrapers / small excavators	*Scarus longipinnis*
Scrapers / small excavators	*Scarus niger*
Scrapers / small excavators	*Scarus oviceps*
Scrapers / small excavators	*Scarus prasiognathos*
Scrapers / small excavators	*Scarus psittacus*
Scrapers / small excavators	*Scarus quoyi*
Scrapers / small excavators	*Scarus rivulatus*
Scrapers / small excavators	*Scarus schlegeli*
Scrapers / small excavators	*Scarus* sp.
Scrapers / small excavators	*Scarus spinus*
Scrapers / small excavators	*Scarus tricolor*
Scrapers / small excavators	*Scarus xanthopleura*
Large excavators / bioeroders	*Bolbometopon muricatum*
Large excavators / bioeroders	*Cetoscarus ocellatus*[2]
Large excavators / bioeroders	*Chlorurus frontalis*[2]
Large excavators / bioeroders	*Chlorurus microrhinos*[2]
Large excavators / bioeroders	*Scarus rubroviolaceus*[2]

[1] *classified as 'browser' until reaches 20 cm in length*
[2] *classified as 'scraper/small excavator' when smaller than 35 cm in length, and 'large excavator/bioeroder' when larger than 35 cm in length*

Reference

Heenan A, Hoey AS, Williams GJ, Williams ID (2016) Natural bounds of herbivorous coral reef fishes. *Proc. R. Soc. B* **283**: 20161716. http://dx.doi.org/10.1098/rspb.2016.1716

Supplementary Table 3 - As part of a sensitivity analysis, 'spatio-physical' models were additionally run using ± 5 and ± 10 humans km^{-2} reef as a threshold from which to categorise 'low' and 'high' impact sites. Notably, site allocations were the same for 30 and 35 humans km^{-2} reef (i.e. no sites had values between 30 and 35 humans km^{-2} reef). Values in tables represent adjusted-R^2 values from GAMM models with structure as described in the manuscript. All outcomes were consistent with those found for the 25 humans km^{-2} reef threshold, indicating the findings are robust.

	Threshold = 15 humans km^{-2} reef		**Threshold = 20 humans km^{-2} reef**	
	low (n=25)	**high (n=37)**	**low (n=27)**	**high (n=35)**
Live hard coral	0.69	0.00	0.49	0.00
Branching	0.66	0.09	0.63	0.07
Massive	0.41	0.00	0.55	0.02
Encrusting	0.09	0.00	0.04	0.00
Turf algae	0.00	0.00	0.00	0.00
Macroalgae	0.63	0.19	0.63	0.16
Dead hard coral	0.21	0.09	0.23	0.03
CCA	0.00	0.00	0.00	0.00
Average	**0.34**	**0.05**	**0.32**	**0.04**
t-test outcome	**0.019**		**0.015**	

	Threshold = 25 humans km^{-2} reef		**Threshold = 30/35 humans km^{-2} reef**	
	low (n=29)	**high (n=33)**	**low (n=34)**	**high (n=28)**
Live hard coral	0.52	0.00	0.50	0.00
Branching	0.64	0.17	0.64	0.01
Massive	0.50	0.10	0.47	0.00
Encrusting	0.19	0.00	0.08	0.06
Turf algae	0.00	0.00	0.00	0.00
Macroalgae	0.59	0.26	0.55	0.23
Dead hard coral	0.33	0.24	0.37	0.17
CCA	0.02	0.00	0.05	0.00
Average	**0.35**	**0.10**	**0.33**	**0.06**
t-test outcome	**0.010**		**0.015**	

Supplementary Table 4 - As an additional analysis, 'spatio-physical' models were run for human density as calculated per *outer reef area* only (i.e. human density per outer reef) using 60, 80 and 100 humans km^{-2} outer reef as thresholds from which to categorise 'low' and 'high' impact sites (note: the thresholds are higher as the area of reef relative to humans is smaller when considering only outer reef). Values in tables represent adjusted-R^2 values from GAMM models with structure as described in the manuscript. All outcomes were consistent with those found for the 25 humans km^{-2} reef threshold, indicating the findings are robust. While certain target fish species only occur on the outer reefs, some of the fishing and gleaning activity to meet protein demands would be focused on areas other than outer reefs. Furthermore, additional impacts by local human populations (in particular nutrient input) would be diluted in cases where large areas of backreef occur. Thus, even though there are trade-offs involved with either calculation of human density, we feel that human density per total reef area is the most appropriate proxy of local human impact, and thus present those values in the main manuscript.

	Threshold = 60 humans km^{-2} outer reef		**Threshold = 80 humans km^{-2} outer reef**	
	low (n=25)	**high (n=37)**	**low (n=32)**	**high (n=30)**
Live hard coral	0.48	0.18	0.38	0.01
Branching	0.33	0.12	0.33	0.20
Massive	0.49	0.08	0.47	0.09
Encrusting	0.00	0.00	0.00	0.00
Turf algae	0.23	0.00	0.15	0.00
Macroalgae	0.39	0.31	0.39	0.21
Dead hard coral	0.28	0.00	0.20	0.02
CCA	0.00	0.03	0.00	0.00
Average	**0.27**	**0.09**	**0.24**	**0.07**
t-test outcome	**0.012**		**0.011**	

	Threshold = 100 humans km^{-2} outer reef	
	low (n=35)	**high (n=27)**
Live hard coral	0.37	0.37
Branching	0.35	0.35
Massive	0.47	0.47
Encrusting	0.00	0.00
Turf algae	0.07	0.07
Macroalgae	0.45	0.45
Dead hard coral	0.20	0.20
CCA	0.01	0.01
Average	**0.24**	**0.02**
t-test outcome	**0.009**	

Supplementary Table 5 - Best-fit model outcomes based on GAMM models (with island cluster as a random effect for all response variables, and surveyor bias as an additional random effect for turf algae). A '+' indicates that the predictor was selected by model selection procedures for the respective row's model. RI values in grey boxes under model selection output (boldface if predictor was selected by model selection procedures for models with Akaike weight >0.05). (A) outcomes for low local impact sites (< 25 humans km^{-2} reef), (B) outcomes for high local impact sites (> 25 humans km^{-2} reef).

(A)

	relief	browsers	depth	detritivores	excavators	gravity	grazers	latitude	scrapers	storms		adj-R2	adj-R2 conditional	df	logLik	AICc	delta	weight
LIVE CORAL	-0.24		+									0.50	0.70	6.00	-13.18	42.20	0.00	0.27
												0.09	0.13	3.00	-18.29	43.50	1.36	0.14
			+						+			0.51	0.70	7.00	-12.19	43.70	1.54	0.13
			+									0.31	0.43	5.00	-15.83	44.30	2.10	0.10
		+										0.33	0.45	5.00	-15.93	44.50	2.29	0.09
	-0.19											0.21	0.29	4.00	-17.86	45.40	3.22	0.05
		+	+									0.48	0.67	7.00	-13.12	45.60	3.39	0.05
	0.42	**0.18**	**0.66**	0.01	0.01	0.01	0.01	0.01	**0.20**	0.01								
BRANCHING CORAL										+		0.55	0.59	5.00	-31.52	75.70	0.00	0.49
				+						+		0.64	0.68	7.00	-28.77	76.90	1.23	0.26
			+							+		0.60	0.63	7.00	-30.50	80.30	4.67	0.05
	0.06	0.02	**0.06**	**0.30**	0.05	0.01	0.02	0.04	0.02	**1.00**								
MASSIVE CORAL									+			0.48	0.51	5.00	-30.20	73.00	0.00	0.32
									+	+		0.60	0.64	7.00	-27.49	74.30	1.31	0.17
		+										0.37	0.40	5.00	-31.87	76.30	3.33	0.06
	-0.21								+			0.50	0.54	6.00	-30.33	76.50	3.46	0.06
	-0.43											0.34	0.37	4.00	-33.51	76.70	3.67	0.05
	0.22	**0.13**	0.03	0.06	0.01	0.05	0.05	0.03	**0.73**	**0.27**								
ENCRUSTING CORAL												0.10	0.12	3.00	-25.28	57.50	0.00	0.63
					+							0.20	0.24	5.00	-24.48	61.60	4.05	0.08
	0.09											0.12	0.14	4.00	-26.12	61.90	4.39	0.07
	0.10	0.01	0.02	0.05	**0.11**	0.01	0.04	0.02	0.02	0.05								
TURF ALGAE												0.18	0.18	4.00	-49.83	109.30	0.00	0.49
				+								0.25	0.26	6.00	-48.22	112.30	2.93	0.11
	-0.19											0.19	0.19	5.00	-49.95	112.50	3.19	0.10
					+							0.21	0.21	6.00	-48.66	113.10	3.81	0.07
	0.15	0.03	0.02	**0.15**	**0.10**	0.05	0.03	0.03	0.03	0.02								
FLESHY ALGAE	-0.83									+		0.50	0.51	6.00	-47.75	111.30	0.00	0.25
	-0.96		+							+		0.64	0.65	8.00	-44.34	111.90	0.58	0.19
	-1.00											0.31	0.32	4.00	-51.89	113.50	2.14	0.09
										+		0.36	0.37	5.00	-50.75	114.10	2.80	0.06
	0.72	0.13	**0.25**	0.03	0.07	0.02	0.02	0.13	0.07	**0.79**								
CCA												0.00	0.00	3.00	-38.85	84.70	0.00	0.55
	-0.25											0.06	0.07	4.00	-38.72	87.10	2.45	0.16
							+					0.03	0.03	5.00	-38.65	89.90	5.26	0.04
	0.22	0.03	0.05	0.02	0.02	0.02	0.06	0.04	0.04	0.03								
DEAD CORAL									+			0.39	0.48	5.00	-20.21	53.00	0.00	0.58
		+							+			0.52	0.64	7.00	-18.26	55.80	2.82	0.14
									+	+		0.51	0.63	7.00	-18.93	57.20	4.16	0.07
	0.06	**0.16**	0.02	0.01	0.01	0.01	0.01	0.01	**0.89**	**0.13**								

(B)

	relief	browsers	depth	detritivores	excavators	gravity	grazers	latitude	scrapers	storms		adj-R2	adj-R2 conditional	df	logLik	AICc	delta	weight
LIVE CORAL												0.06	0.08	3.00	-23.00	52.90	0.00	0.44
	-0.25											0.15	0.20	4.00	-22.47	54.40	1.57	0.20
							+					0.21	0.28	5.00	-21.28	54.90	2.00	0.16
	0.25	0.03	0.04	0.02	0.01	0.05	**0.23**	0.04	0.01	0.01								
BRANCHING CORAL												0.03	0.04	3.00	-50.81	108.50	0.00	0.32
	-0.51											0.11	0.11	4.00	-49.80	109.10	0.60	0.23
				+								0.11	0.11	5.00	-49.71	111.70	3.25	0.06
	0.41	0.03	0.03	**0.13**	0.03	0.06	0.05	0.04	0.03	0.12								
MASSIVE CORAL												0.34	0.35	3.00	-47.54	101.90	0.00	0.34
									+			0.42	0.43	5.00	-46.27	104.80	2.91	0.08
	0.19											0.35	0.36	4.00	-47.71	104.90	2.96	0.08
							+					0.40	0.42	5.00	-46.42	105.10	3.20	0.07
			+									0.38	0.39	5.00	-46.42	105.10	3.21	0.07
				+								0.38	0.39	5.00	-46.46	105.20	3.29	0.07
	0.16	0.03	**0.12**	**0.12**	0.07	0.02	**0.12**	0.08	**0.14**	0.03								
ENCRUSTING CORAL												0.03	0.03	3.00	-40.01	86.90	0.00	0.25
						+						0.25	0.27	5.00	-37.35	87.00	0.13	0.24
				+								0.21	0.23	5.00	-38.19	88.70	1.81	0.10
		+				+						0.40	0.44	7.00	-35.19	89.00	2.17	0.09
	0.20											0.06	0.07	4.00	-40.20	89.90	3.01	0.06
	0.15	**0.15**	0.02	**0.19**	0.03	**0.42**	0.02	0.03	0.03	0.02								
TURF ALGAE												0.53	0.55	4.00	-44.78	99.00	0.00	0.62
	-0.04											0.53	0.55	5.00	-45.42	103.20	4.10	0.08
							+					0.58	0.60	6.00	-44.01	103.40	4.33	0.07
	0.11	0.02	0.06	0.04	0.03	0.02	**0.10**	0.03	0.02	0.02								
FLESHY ALGAE												0.06	0.06	3.00	-54.46	115.80	0.00	0.33
	-0.54											0.15	0.15	4.00	-53.49	116.50	0.69	0.23
		+										0.11	0.11	5.00	-53.43	119.20	3.39	0.06
	0.36	**0.10**	0.03	0.07	0.03	0.04	0.04	0.07	0.06	0.07								
CCA												0.05	0.06	3.00	-28.76	64.40	0.00	0.44
		+										0.26	0.31	5.00	-26.36	65.00	0.65	0.32
	-0.07											0.06	0.07	4.00	-29.70	68.90	4.51	0.05
	0.08	0.38	0.02	0.02	0.02	0.05	0.01	0.02	0.02	0.02								
DEAD CORAL												0.00	0.00	3.00	-8.94	24.70	0.00	0.79
	0.00											0.00	0.00	4.00	-10.73	30.90	6.20	0.04
								+				0.10	0.28	5.00	-9.38	31.10	6.33	0.03
	0.04	0.03	0.02	0.01	0.02	0.01	0.03	0.04	0.02	0.01								